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The Systematics and Distributional Ecology of the Superfamily Ampeliscoidea (Amphipoda: Gammaridea) in the Northeastern Pacific Region.

II. The Genera *Byblis* and *Haploops*

John J. Dickinson

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Nat Sci. #1
250

Ottawa 1983

Publications in
Natural Sciences, No. 1

THE SYSTEMATICS AND DISTRIBUTIONAL ECOLOGY OF THE SUPERFAMILY AMPELISCOIDEA (AMPHIPODA: GAMMARIDEA) IN THE NORTHEASTERN PACIFIC REGION. II. THE GENERA *BYBLIS* AND *HAPLOOPS*.

John J. Dickinson
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Publications de
sciences naturelles, n° 1

Musées nationaux
du Canada

Musée national
des sciences naturelles

91-01895/

PUBLICATIONS IN NATURAL SCIENCES supersedes the following series: *Publications in Biological Oceanography* (final issue, No. 11); *Publications in Botany* (final issue, No. 13); *Publications in Palaeontology* (final issue, No. 6); *Publications in Zoology* (final issue, No. 17).

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National Museum of Natural Sciences
Publications in Natural Sciences, No. 1

Published by the
National Museums of Canada

©National Museums of Canada 1983

National Museum of Natural Sciences
National Museums of Canada
Ottawa, Canada

Catalogue No. NM. 95-43/1

Printed in Canada

ISBN 0-662-11271-7
ISSN 0714-0983

Musée national des sciences naturelles
Publications de sciences naturelles, n° 1

Publié par les
Musées nationaux du Canada

©Musées nationaux du Canada 1983

Musée national des sciences naturelles
Musées nationaux du Canada
Ottawa, Canada

N° de catalogue NM. 95-43/1

Imprimé au Canada

ISBN 0-662-11271-7
ISSN 0714-0983

Contents

Abstract, iv
Résumé, v
Legend for all figures, vi
Introduction, 1
Materials, 2
Systematic Section, 3
  Superfamily Ampeliscoidea Bousfield 1978, 3
  Family Ampeliscidae Bate 1857, 3
  Key to the Ampeliscidae of the Northeastern Pacific Region, 3
  Genus *Byblis* Boeck 1871, 3
    Key to the Northeastern Pacific *Byblis* (Females and Subadult Males), 3
    Byblis gaimardi (Krøyer) 1847, 4
    Byblis longispina n. sp., 7
    Byblis mulleni n. sp., 9
    Byblis millsi n. sp., 11
    Byblis thyablis J.L. Barnard 1971, 14
    Byblis bathyalis J.L. Barnard 1966, 16
    Byblis barbarensis J.L. Barnard 1960, 16
    Byblis sp. nr. *crassicornis*, 16
    Byblis teres J.L. Barnard 1967, 16
    Byblis tannerensis J.L. Barnard 1966, 17
    Byblis veleronis J.L. Barnard 1954, 17
    Byblis pearcyi n. sp., 17
    Byblis breviramus n. sp., 20
  Genus *Haploops* Liljeborg 1856, 22
    Key to Species of *Haploops* of the Northeastern Pacific Region, 22
    Haploops tubicola Liljeborg 1856, 23
    Haploops laevis Hoek 1882, 24
    Haploops sibirica Gurjanova 1929, 27
    Haploops lodo J.L. Barnard 1961, 27
    Haploops setosa Boeck, 1871, 27
Discussion, 28
Acknowledgements, 31
Tables
  Table 1: List of Characters Used in Cluster Analysis of Northeast Pacific *Byblis* , 32
  Table 2: Data Matrix of *Byblis* spp. versus Character States, 33
  Table 3: Geographical Distribution of *Byblis* spp. in the Northeast Pacific Region, 33
  Table 4: Geographical Distribution of *Haploops* spp. in the Northeast Pacific Region, 34
  Table 5: List of Characters for Analysis of Genera of Ampeliscidae, 35
  Table 6: Multiple Character Analysis of Plesio-apomorphic Trends of Generic Characters in the Family Ampeliscidae, 36
References, 37

Submitted for publication: April 5, 1982
Accepted for publication: August 11, 1982

Abstract

The genus *Byblis* is represented by eight species on the North American continental shelf in the region between the Bering Sea and northern California. ***Byblis pearcyi*** new species and ***Byblis breviramus*** new species are described from the St. Lawrence Island region of the Bering Sea. ***Byblis longispina*** new species and ***Byblis mulleni*** new species, both closely related to *Byblis gaimardi* (Krøyer) are described from the Gulf of Alaska and the Queen Charlotte Islands respectively. ***Byblis millsi*** new species is described from the Strait of Juan de Fuca, but it occurred from northern British Columbia to Southern California. The range of *Byblis gaimardi* (Krøyer) is extended south into the Bering Sea. The range of *Byblis thyablis* J.L. Barnard is extended north to the Queen Charlotte Islands. A key to the species of *Byblis* from the northeast Pacific region includes five additional deep water species which may occur in the study area. A cluster analysis of northeast Pacific *Byblis* suggested possible subgeneric groupings. However, no formal attempt is made to subdivide *Byblis* since the generic characters vary little and those that do vary show a mosaic distribution. The genus *Haploops* is represented by two arctic-boreal species, *Haploops tubicola* Liljeborg and *Haploops laevis* Hoek. A key to the species of *Haploops* includes four other species which are likely to occur in the region.

Résumé

Le genre *Byblis* est représenté par huit espèces sur le plateau continental d'Amérique du Nord, dans la région qui va de la mer de Béring au nord de la Californie. ***Byblis pearcyi***, nouvelle espèce, et ***Byblis breviramus***, nouvelle espèce, sont décrites d'après des spécimens provenant de la région de l'île St. Lawrence, dans la mer de Béring. ***Byblis longispina***, nouvelle espèce, et ***Byblis mulleni***, nouvelle espèce, toutes deux étroitement apparentées à *Byblis gaimardi* (Krøyer), sont décrites d'après des spécimens provenant du golfe de l'Alaska et de l'archipel de la Reine-Charlotte, respectivement. ***Byblis millsi***, nouvelle espèce, est décrite d'après des spécimens provenant du détroit de Juan de Fuca, mais on l'a rencontrée depuis le nord de la Colombie-Britannique jusqu'au sud de la Californie. L'aire de répartition de *Byblis gaimardi* (Krøyer) est reculée vers le sud jusque dans la mer de Béring; celle de *Byblis thyablis* J.L. Barnard est reculée vers le nord jusque dans l'archipel de la Reine-Charlotte. La clef des espèces de *Byblis* du nord-est du Pacifique comprend cinq autres espèces d'eau profonde qui se trouvent probablement dans la région intéressée par notre étude. Par ailleurs, l'analyse de grappes des espèces de *Byblis* se trouvant dans le nord-est du Pacifique a indiqué la possibilité d'établir des groupements par sous-genres. Toutefois, aucune tentative n'est faite expressément pour subdiviser *Byblis*, étant donné que les caractères génériques varient très peu, et que les exceptions présentent une répartition en mosaïque. Le genre *Haploops* est représenté quant à lui par deux espèces boréales-arctiques, *Haploops tubicola* Liljeborg et *Haploops laevis* Hoek. La clef des espèces de *Haploops* comprend encore quatre espèces que l'on peut vraisemblablement rencontrer dans la région.

LEGEND FOR ALL FIGURES

Hd	head
Gn	gnathopod
P	peraeopod
Cx	coxal plate
U	uropod
T	telson
UL	upper lip
LL	lower lip
Md	mandible
Lft	left
Rt	right
Mx	maxilla
Mxpd	maxilliped

Introduction

The family Ampeliscidae is represented in the near shore waters of the northeast Pacific region by three genera: *Ampelisca*, *Byblis*, and *Haploops*. The systematics of the genus *Ampelisca* from this region and the general biology of the family were treated in a previous paper (Dickinson 1982). Barnard (1954, 1960, 1966, 1967b, 1971) described a number of species in the genera *Byblis* and *Haploops* from Oregon and California waters, but no formal taxonomic studies have been made on these genera in British Columbian and Alaskan waters.

The bathymetry and feeding ecology of species in the genera *Byblis* and *Haploops* are generally poorly known. As noted by Mills (1971), species in these two genera tend to occur at greater depths than species of *Ampelisca*. The majority of *Ampelisca* species occur at depths less than 100 m, whereas most species of *Byblis* and *Haploops* are found at depths greater than 100 m. All species of *Byblis* and *Haploops* are presumed to be tube-dwelling detritivores, but no direct observations of their feeding biology have been recorded since the studies of Enequist (1949) on *Haploops tubicola* Liljeborg and *Byblis gaimardi* (Krøyer).

In general, little is known about the life histories of species of *Byblis* and *Haploops*. Kanneworf (1966) demonstrated that European populations of *Haploops tubicola* Liljeborg and *Haploops tenuis* Kanneworf took 2–3 years to reach breeding size. Bousfield (1973) believed the western Atlantic species, *Byblis serrata* Smith, to be an annual. It seems probable that most species of *Byblis* and *Haploops* living in arctic or bathyal waters take several years to reach maturity, but no data exist.

The present study treats the systematics and distributional ecology of the genera *Byblis* and *Haploops*. Combined with the previous study on the genus *Ampelisca* (Dickinson 1982), it attempts to fill in a major gap in the knowledge of the family Ampeliscidae from the coastal waters of British Columbia, southeast Alaska, and the Bering Sea. It is hoped that these studies will stimulate future investigations on the ecology of the species in this family which are an important component in the benthic ecosystem of the region. Also, some of the methods and insights from these studies may prove useful to workers studying the Ampeliscidae of other regions.

Materials

This study was based primarily on collections in the Canadian National Museum of Natural Sciences. These collections range from southeast Alaska to Oregon, but are most extensive for British Columbia. The primary source of this material was a series of field expeditions conducted by Dr. E.L. Bousfield and colleagues at the N.M.N.S.. Station data for expeditions to southern Vancouver Island (1955), Queen Charlotte Islands (1957), northern Vancouver Island (1959), southeastern Alaska (1961), and northcentral British Columbia (1964) were published previously (Bousfield 1957; Bousfield 1963; Bousfield and McAllister 1962; and Bousfield 1968). Data for expeditions to Washington and Oregon (1966), southern Vancouver Island and Burrard Inlet (1970, 1975, 1976, 1977, 1978), and southeastern Alaska (1980) may be found in Bousfield and Jarrett (1981).

Other major sources of material used in this study were collections donated to the N.M.N.S. by Dr. Colin Levings of the Pacific Environmental Institute, Dr. Peter Slattery of the Moss Landing Marine Laboratory, Dr. Mary Nerini of the N.O.A.A. Marine Mammal Laboratory in Seattle, Mauseth Associates in Seattle, and Marjorie Bousfield of Dalhousie University. Specimens were borrowed from Dr. A.G. Carey of Oregon State University, Dr. Richard Brusca of the Allan Hancock Foundation, Dr. K.O. Coyle of the University of Alaska Museum, Peter Lambert of the British Columbia Provincial Museum, and Joan Ellis of the British Museum (Natural History).

Preserved material and prepared slide mounts are housed in the National Museum of Natural Sciences, Ottawa, and representative specimens are also deposited in the collections of the U.S. National Museum, Washington D.C..

Systematic Section

Superfamily Ampeliscoidea Bousfield 1978
Family Ampeliscidae Bate 1857
:Stebbing 1906, pp. 97–98
:J.L. Barnard 1969, p. 128
:Bousfield 1973, p. 132; 1982a, p. 278

A Key to the Ampeliscidae of the Northeastern Pacific Region

1. Head as deep as long; basal lobe of peraeopod 7 not expanded distally, posterior margin nearly vertical ..... *Haploops* (p. 22)
   Head longer than deep; basal lobe of peraeopod 7 expanded distally, posterior margin oblique 2
2. Anteroventral corner of head excavate for insertion of antenna 2; dactyls of peraeopods 5–6 simple; anterior margin of basal lobe of peraeopod 7 fully setose near its junction with segment 3; dactyl of peraeopod 7 reduced to a spine ..... *Byblis* (p. 3)
   Anteroventral corner of head not excavate; dactyls of peraeopods 5–6 hook-like; anterior margin of basal lobe of peraeopod 7 lacking setae near its junction with segment 3; dactyl of peraeopod 7 broad at base, not spine-like. ..... *Ampelisca* (see Dickinson 1982)

Genus ***Byblis*** Boeck 1871
:Stebbing 1906, pp. 111–112
:J.L. Barnard 1969, p. 130
:Bousfield 1973, p. 137

Diagnosis

Head longer than deep, narrowing anteriorly with anteroventral corner excavate for insertion of antenna 2. Eyes (when present) have lenses in both dorsofrontal and ventrofrontal pairs. Antenna 2, flagellum with more than five segments. Mandibular palp, segment 3 much shorter than segment 2. Maxilliped, inner plate slender and slightly elongate. Anterior coxae slightly longer than broad. Coxa 4, broader than long, posterior lobe acutely produced. Peraeopods 3–4, segment 5 not greatly reduced in length. Peraeopods 5–6, dactyls medium length and simple. Basal lobe of peraeopod 7, expanded distally, posterior margin oblique, and anterior margin fully setose near junction with segment 3. Peraeopod 7, dactyl reduced to a spine. Uropod 3, medial margins of rami usually serrate. Telson, short in female and elongate in pelagic stage males, cleft varies from 1/4 to 3/4 length.

Remarks

The diagnoses of *Byblis* and *Haploops* given in this paper parallel that given for *Ampelisca* in Dickinson (1982). These diagnoses utilize a broader suite of characters than Barnard (1969), and are more precise than Bousfield (1973).

Barnard (1969) reported 21 species of *Byblis* in his world-wide treatment of marine gammarideans. Subsequent work by Barnard (1967a,b; 1971), Margulis (1967), Just (1970), Mills (1971), and this paper will bring the number of described species of *Byblis* close to 40. Many *Byblis* spp. probably remain to be described from the deep sea and arctic basin.

A Key to Northeastern Pacific *Byblis* (Females and Subadult Males)

1. Anterior margin of segment 4 of peraeopod 7 with three or more long spines; telson cleft 1/4 or less of length 2
   Anterior margin of segment 4 of peraeopod 7 with a single long spine; telson cleft 1/3 or more of length 4
2. Antenna 1 just reaching end of peduncle of antenna 2; telson apical spines very long, about 1/2 length of telson ..... *Byblis longispina* n. sp. (p. 7)
   Antenna 1 extending beyond end of peduncle of antenna 2; telson apical spines medium length, 1/3 or less of telson 3

3. Uropod 2 long, extending well beyond tip of uropod 1; telson apical spines about 1/3 telson length ..... *Byblis mulleni* n. sp. (p. 9)
Uropod 2 medium length, just reaching end of uropod 1; telson apical spines about 1/4 telson length ..... *Byblis gaimardi* (Krøyer) (p. 4)
4. Anterior margin of segment 6 of peraeopod 7 bearing two or more rows of comb spines; telson apices scalloped 5
Anterior margin of segment 6 of peraeopod 7 lacking comb spines; telson apices broadly or acutely rounded 9
5. Posterodistal corner of coxae 2–3 obliquely truncated; ventral margin of coxae 1–3 very weakly serrated ..... *Byblis veleronis* J.L. Barnard (p. 17)
Posterodistal corner of coxae 2–3 not truncated; ventral margin of coxae 1–3 strongly serrated 6
6. Antenna 1 extending well beyond end of peduncle of antenna 2 7
Antenna 1 just reaching end of peduncle of antenna 2 8
7. Peduncle of antenna 1 does not extend beyond the end of segment 4 of antenna 2; segment 6 of peraeopod 7 has two rows of comb spines on anterior margin ..... *Byblis thyablis* J.L. Barnard (p. 14)
Peduncle of antenna 1 extends beyond the end of segment 4 of antenna 2; segment 6 of peraeopod 7 has three rows of comb spines on anterior margin ..... *Byblis bathyalis* J.L. Barnard (p. 16)
8. Eyes well developed; rami of uropod 1 subequal in length ..... *Byblis millsi* n. sp. (p. 11)
Eyes lacking; inner ramus of uropod 1 distinctly shorter than outer ramus ..... *Byblis barbarensis* J.L. Barnard (p. 16)
9. Coxae 2–3 truncated distally; peduncle of antenna 1 extending beyond segment 4 of antenna 2; segments 5–6 of peraepod 7 slender and sparsely spinulose 10
Coxae 2–3 not distally truncated; peduncle of antenna 1 not reaching end of segment 4 of antenna 2; segments 5–6 of peraeopod 7 relatively stout and strongly spinulose 12
10. Medial margin of rami of uropod 3 multiserrated ..... *Byblis tannerensis* J.L. Barnard (p. 17)
Medial margin of rami of uropod 3 with single or no serrations 11
11. Antenna 1 long, nearly equal to antenna 2 in length; uropod 3 with single serration on medial margin of rami; telson apical spines short ..... *Byblis* sp. (nr. *crassicornis*) (p. 16)
Antenna 1 short, just reaching peduncle of antenna 2; rami of uropod 3 lacking medial serrations; telson apical spines long ..... *Byblis teres* J.L. Barnard (p. 16)
12. Coxa 1, posterodistal corner obliquely truncated; uropod 2, rami distinctly shortened; telson, basal width greater than length ..... *Byblis breviramus* n. sp. (p. 20)
Coxa 1, posterodistal corner not truncated; uropod 2 rami normal length; telson, basal width subequal to length ..... *Byblis pearcyi* n. sp. (p. 17)

Byblis gaimardi (Krøyer) 1847
Figures 1, 2 & 3 (in part)

Byblis gaimardi G.O. Sars, 1895, pp. 183–184, pl. 64
:Stebbing, 1906, p. 113
:Mills, 1971, pp. 367–370, figs. 6–7
:Lincoln, 1979, p. 122, fig. 52

Material examined

Labrador, Nain Bay, 56°31.3'N, 61°00.2'W, 76–128, 26 October 1973, fine sand, collected by E.L. Mills (1 mat. ♀, 4 subad. ♀♀, 5 subad, ♂♂, 50 juv.).

Alaska, Bering Sea, St. Lawrence Island, 63°45'N, 168°05'W, 33 m, 12 June 1980, collected by U.S. Bureau of Land Management (3 br. II ♀♀, 5 subad. ♀♀, 13 subad. ♂♂); same station, July 1980 (5 ov. ♀♀). Aleutians, U. of Alaska collections, 56°06'N, 166°58'W, 68 m, 16 June 1975 (1 br. II ♀♀, 2 subad. ♂♂); 56°55.4'N, 170°56.6'W, 110 m, 11 May 1975 (1 br. II ♀); 57°24'N, 167°10'W, 21 May 1975 (2 adult ♂♂).

Diagnosis

(Female): A deep bodied, medium sized *Byblis* (16–20 mm) characterized by: head, anterior margin weakly produced below insertion of antenna 1, eyes present and well developed. Antenna 1, peduncle medium length extending 2/3 length of peduncular segment 4 of antenna 2, flagellum medium length extending beyond end of peduncle of antenna 2. Antenna 2, about body length, cone gland on peduncular segment 2

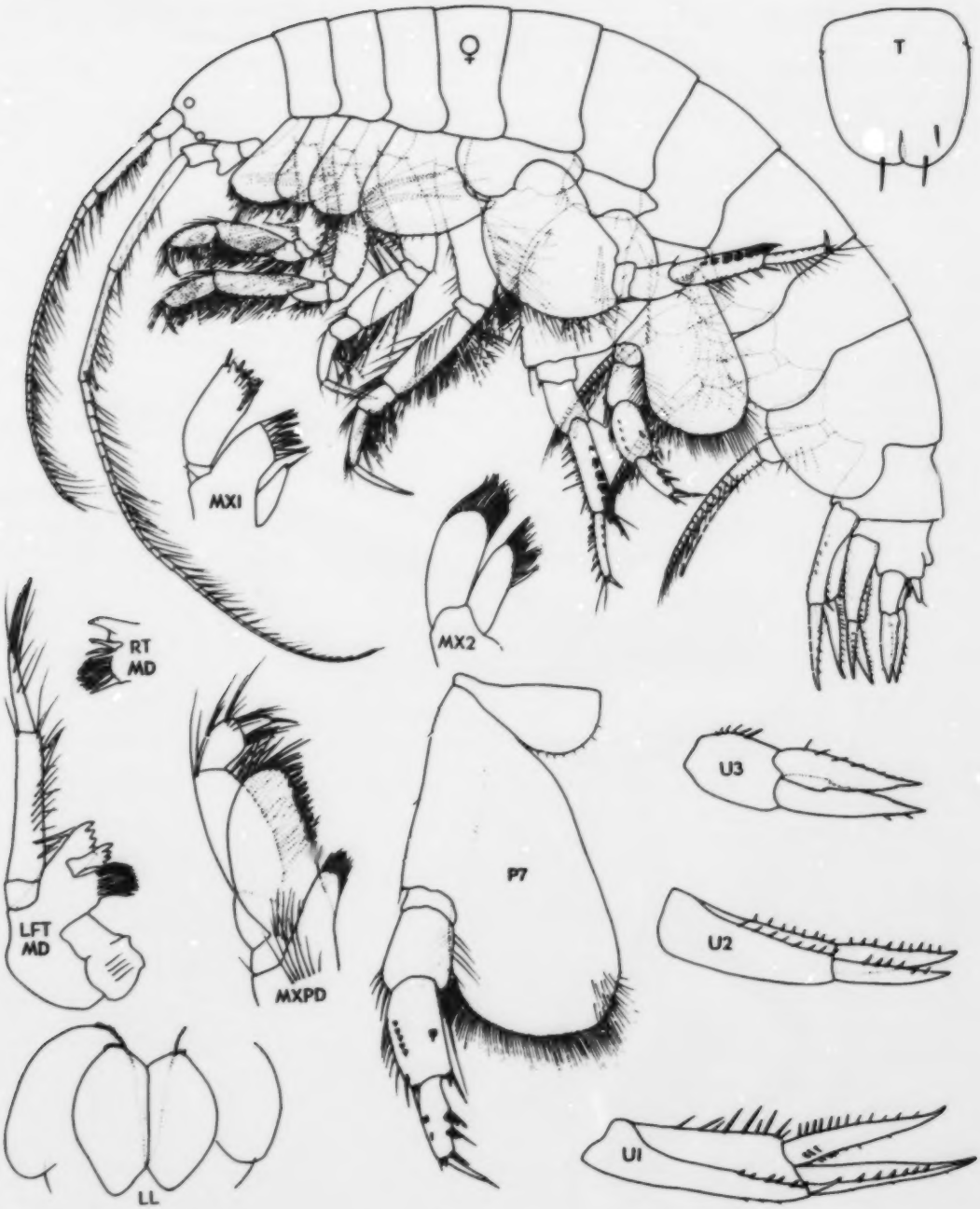

Figure 1. *Byblis gaimardi* (Krøyer). St. Lawrence Island, Bering Sea, Alaska. ♀ 15 mm, subadult.

rounded. Ventral margins of anterior coxae lacking serrations. Coxa 1, strongly expanded distally, posterodistal margin weakly truncated. Coxae 2–3, posterodistal corner not strongly oblique. Coxa 4, posterior tooth moderately produced. Gnathopods 1–2, posterodistal margin of basis serrate. Peraeopod 6, segment 5 lacking anterior comb spines. Peraeopod 7, segment 4 bearing three or more long spines on distal portion of anterior margin, segment 6 lacking strong spination on anterior margin. Pleonal epimeron 1–2, ventral margin with a few short setae. Uropod 1, rami subequal in size and length, both rami spinulose. Uropod 2, medium length reaching tip of uropod 1, rami about 60% length of peduncle. Uropod 3, mid portion of medial margin of both rami serrate. Telson, length subequal to basal width, barely tapering distally, apices rounded with apical spines about 1/4 telson length, cleft about ¼ length. Gills long, thin club-shaped sacs in mature females.

(Male): Pelagic males (16–20 mm) are characterized by: presence of brush setae on peduncles and elongation of the flagellum of both antenna 1 and 2, very short flagellar setae; gills thick, broadly lanceolate, transversely pleated; urosomite 1, dorsal surface slightly raised; uropod 3, rami elongate and more finely serrate on medial margin, inner margin of inner ramus setose; telson elongate, cleft 1/3, spines short and subapical.

Distributional Ecology

Geographic Range: Circumpolar, through the North Atlantic and Arctic oceans and into the Bering Sea (Mills, 1971; Lincoln, 1979). Bathy-

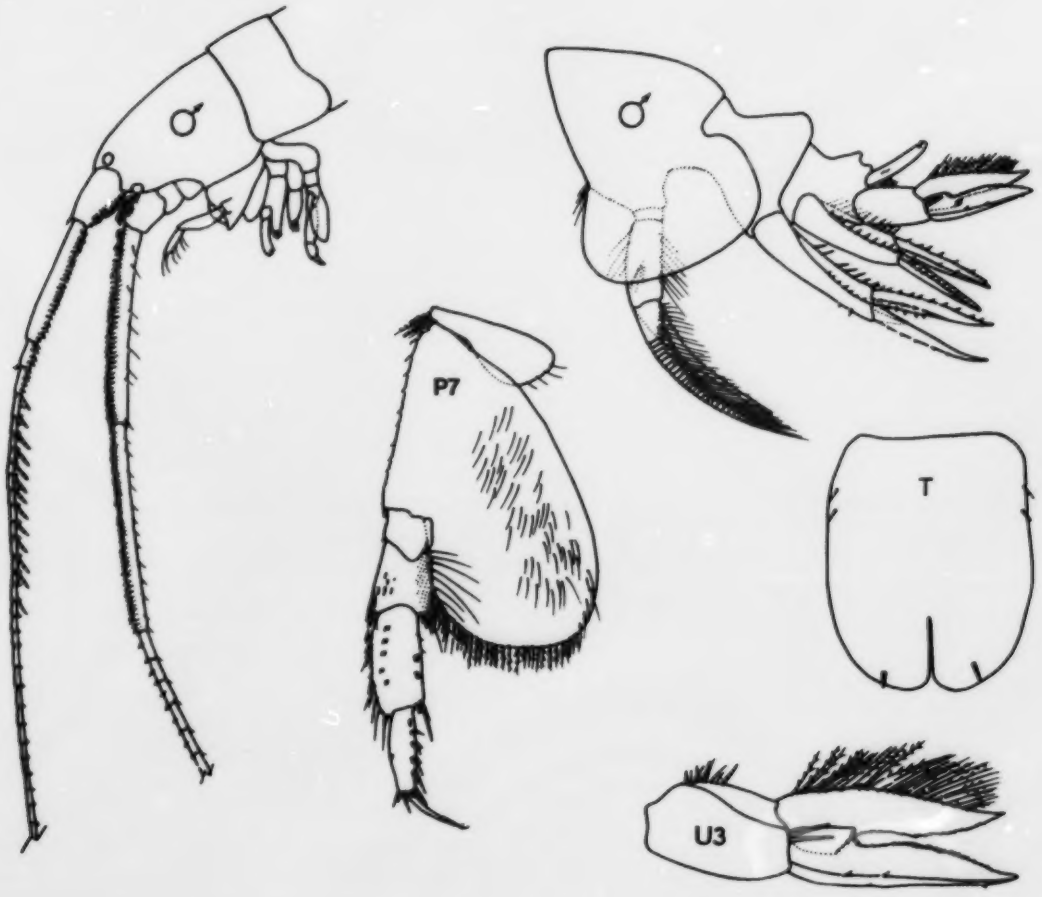

Figure 2. *Byblis gaimardi* (Krøyer). Southern Bering Sea, Alaska. Adult ♂ 17 mm.

metric Range: 5–575 m (Mills 1971). Sediment Preference: fine sand to silt-clay (Lincoln 1979).

Life Cycle

Ovigerous females found in northern Bering Sea in July. Pelagic males found in southern Bering Sea in May.

Remarks

The name *Byblis gaimardi* probably conceals a complex of species. This study represents only a start at unraveling this complex since other forms near "gaimardi" are known to exist in the arctic basin (Just 1980).

Byblis longispina n. sp.
Figures 3 (in part) & 4

Material Examined

Alaska: Gulf of Alaska, Bousfield 1961 stns. A141, Hanning Bay, Montague Island (59°58′N, 147°42′W), 13 July, 21 m, muddy sand, holotype Br. II ♀ (NMC-C-1982-22); A135, Head of Thumb Bay, Resurrection Bay (60°2′N, 149°23′W), 11 July, 24 M, glacial mud, paratype ♂, 8 mm (NMC-C-1982-23).

Diagnosis

(Female): A medium sized *Byblis* (12 mm) characterized by: anterior margin of head produced acutely below insertion of antenna 1, eyes present and well developed. Antenna 1, peduncle medium length extending 2/3 length of segment 4 of antenna 2, peduncular segment 2 very slender and sparsely setose, flagellum short just reaching end of peduncle of antenna 2. Antenna 2, about 2/3 length of body, antennal cone gland on peduncular segment 2 rounded. Coxa 1, strongly expanded distally, posterodistal margin weakly truncated obliquely. Ventral margins of anterior coxae smooth. Coxae 2–3, posterodistal corner not oblique. Coxa 4, posterior tooth moderately and subacutely produced. Gnathopods 1–2, posterodistal margin of basis weakly serrate. Peraeopod 6, segment 5 lacking anterior comb spines. Peraeopod 7, segment 4 with three or more long spines on anterodistal margin, segment 6 lacking strong spination on anterior margin. Pleonal epimeria 1–2, ventral margin with a few short setae. Uropod 1, rami sub-equal in size and length, both margins of inner ramus and outer margin of outer ramus spinulose. Uropod 2, medium length extending just beyond tip of

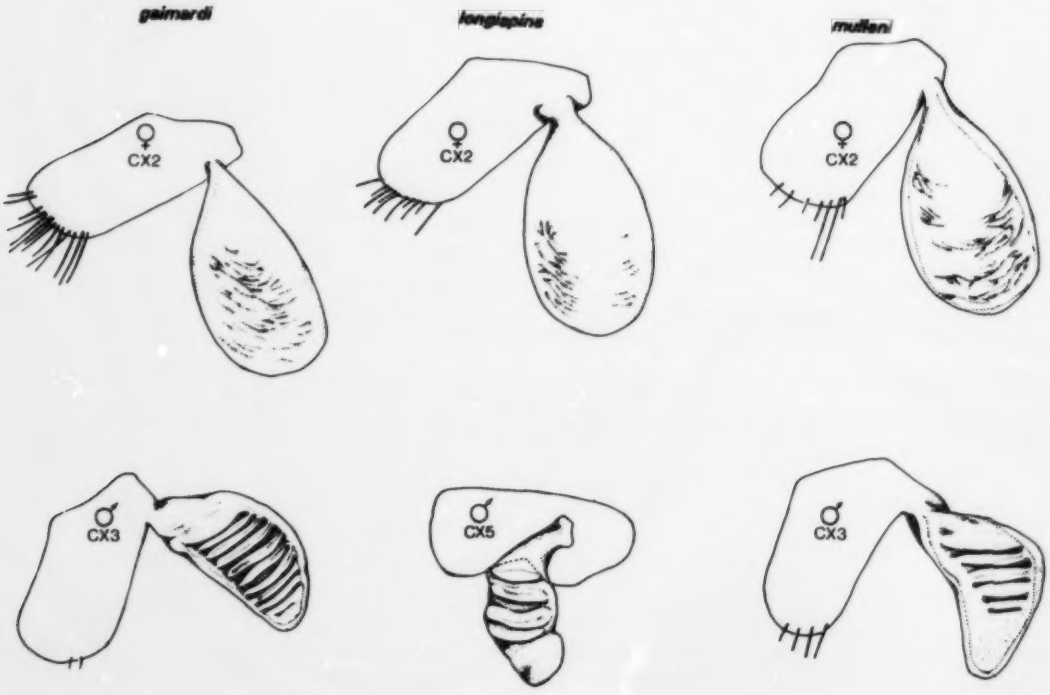

Figure 3. Representative coxal gills of *Byblis gaimardi*, *Byblis longispina*, and *Byblis mulleni*.

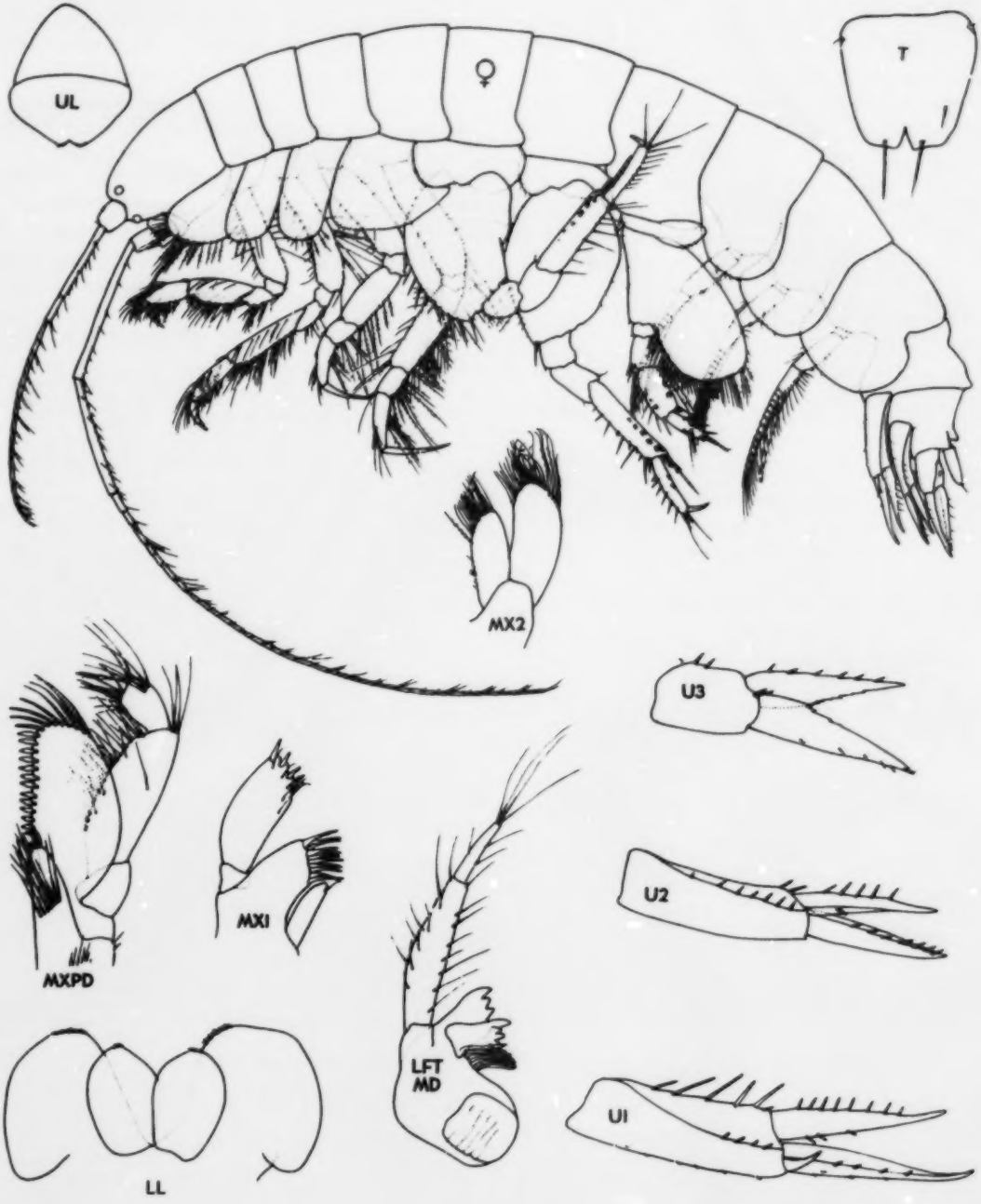

Figure 4. *Byblis longispina* n. sp. Resurrection Bay, Gulf of Alaska. holotype ♀ 12 mm.

uropod 1. Uropod 3, outer ramus slightly longer than inner ramus, mid portion of medial margin of both rami serrate. Telson, length equals basal width, tapering gently distally, cleft only 1/5 length, apices blunt with long apical spines (about 50% telson length) which are set close together. Gills long, thin and unpleated in br. II female.

(Male): No pelagic stage males in N.M.N.S. collections. Gills in subadult male thicker, broadly lanceolate, and pleated.

Etymology

The species name recognizes the very long apical spines of the telson.

Distributional Ecology

Known only from two stations in the Gulf of Alaska.

Remarks

This species is very similar to *B. gaimardi* but differs in its shorter antenna 1, smaller size, and longer apical spines on the telson (see key p. 3 and Fig. 17).

Byblis mulleni n. sp.
Figures 3 (in part) & 5

Material examined

British Columbia, Queen Charlotte Islands, J.W. Scoggan 1965 stn. 105, 54°27'N, 131°42'W, 270 m, holotype ov. ♀, 15 mm (NMC-C-1982-24), paratypes 1 ov. ♀ and 1 subad. ♂ (NMC-C-1982-25). Queen Charlotte Sound, 51°23'N, 129°08'W, 175 m, 14 August 1967, N.A. Powell collector (3 adult ♂♂).

Oregon, Newport, Oregon State University Benthic Invertebrate Catalogue #01341, 44°39.1'N, 124°37.7'W, 225 m, 26 October 1963, Anchor Dredge, A.G. Carey collector (1 ov. ♀, 1 subad. ♀, 1 subad. ♂).

Diagnosis

(Female): A slender bodied, medium-sized *Byblis* (15 mm) characterized by: head, anterior margin acutely produced below insertion of antenna 1, eyes present and well developed. Antenna 1, peduncle medium length extending 2/3 length of peduncular segment 4 of antenna 2, flagellum medium length extending beyond end peduncle of antenna 2. Antenna 2, about 3/4 body length, cone gland on peduncular segment 2 rounded. Coxa 1, moderately expanded distally, posterodistal margin weakly truncated obliquely. Coxae 2–3, posterodistal corner not strongly oblique. Coxa 4, posterior tooth moderately produced. Anterior coxae, ventral margins smooth. Gnathopods 1–2, posterodistal margin of basis serrated. Peraeopod 6, segment 5 lacking anterior comb spines. Peraeopod 7, segment 4 bearing three or more long spines on anterodistal margin, segment 6 lacking strong spination on anterior margin. Pleonal epimeria 1–2, ventral margin with a few short setae. Uropod 1, rami subequal in size and length, both rami spinulose. Uropod 2, long extending beyond tip of uropod 1, rami 80% the length of the peduncle. Uropod 3, outer ramus slightly longer than inner, medial margin of both rami serrated. Telson, length subequal to basal width, gently tapering distally, apices rounded bearing spines about 1/3 telson length, cleft about 1/4 length. Gills long, thin, club-shaped sacs in mature females.

(Male): The pelagic males used for this diagnosis are badly damaged and their identity cannot be certain. Hence, they were not designated on allotypes. Pelagic males differ from females in: antenna 1 elongate, peduncles of both antenna 1 and 2 bear brush setae; gills shorter, thicker, broadly lanceolate, and transversely pleated; urosomite 1, dorsal surface slightly produced; uropod 3, rami elongate with medial margin more finely serrate; telson elongate about 1½ times width with short subapical spines.

Etymology

This species is named after Dr. Michael Mullen of the Scripps Institute of Oceanography who taught me the importance of species biology in trying to understand ecosystems.

Distributional Ecology

Geographic Range: Queen Charlotte Islands to Oregon. Bathymetric Range: 175–270 m.

Life Cycle

Ovigerous females found in: August, October. Pelagic males found in: August.

Remarks

Byblis mulleni is very similar to *B. gaimardi*, but differs in its more slender body, longer uropod 2, and longer telson apical spines (see key p. 4 and Fig. 17).

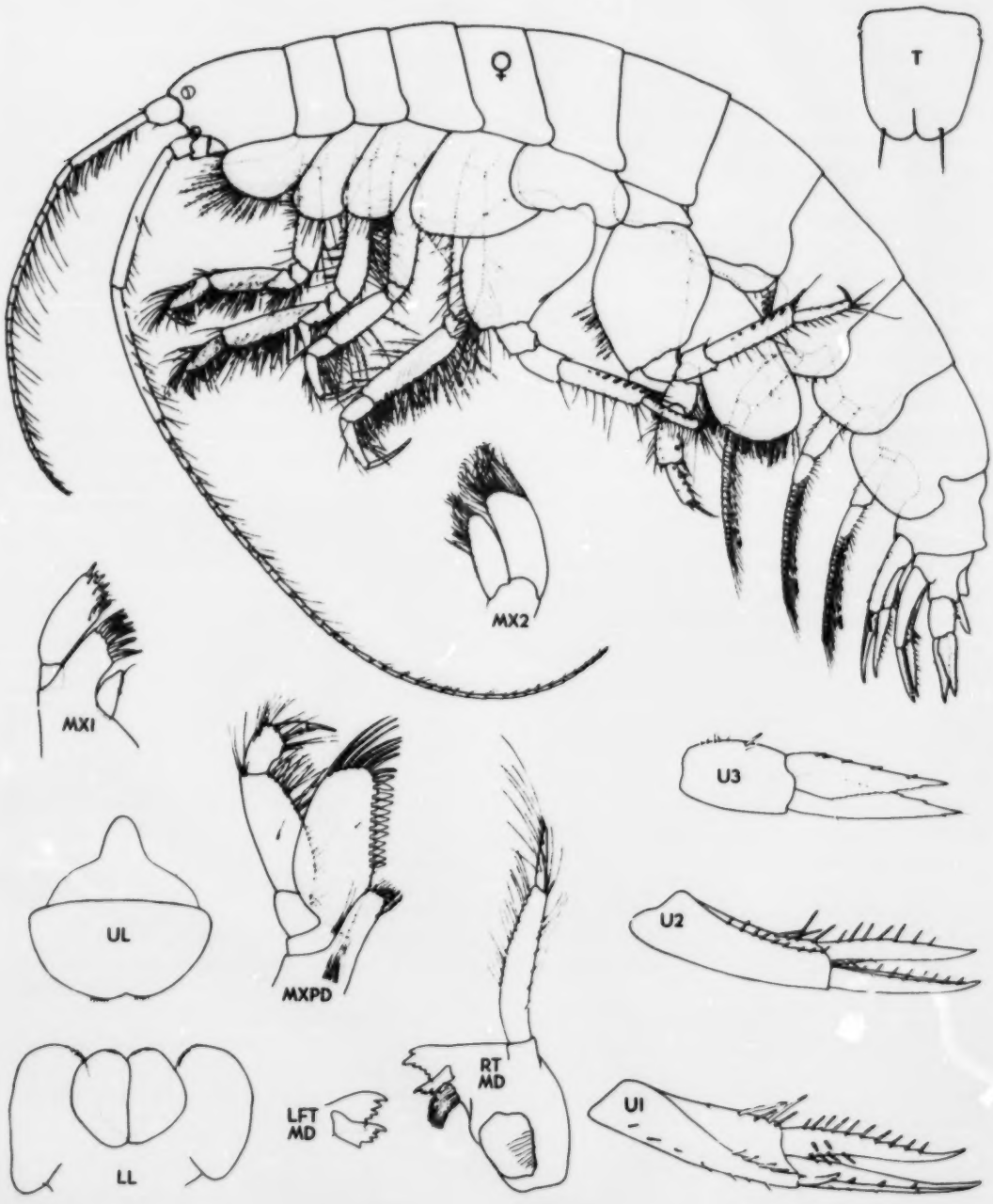

Figure 5. *Byblis mulleni* n. sp. Dixon Entrance, Queen Charlotte Islands, B.C. holotype ♀ 15 mm, ov.

Byblis millsi n. sp.
Figures 6, 7 & 8 (in part)

Material examined

Washington, Strait of Juan de Fuca, Bousfield 1966 stn. W39, Neah Bay, 48°22′N, 124°36′W, muddy sand, low water, 11.8°C, 32.7 o/oo, holotype ov. ♀ 8 mm (NMC-C-1982-19), allotype adult ♂ 8 mm (NMC-C-1982-20), paratypes 25 ♀♀, 15 ♂♂, 5 juveniles (NMC-C-1982-21). Additional Material: **British Columbia**, Queen Charlotte Islands, J.W. Scoggan 1965 stn. 106 (2 ov. ♀♀, 2 subad. ♂♂). North Central Coast, Bousfield 1964 stns. H21, H28, H34, H36, H37, H52 (2 ov. ♀♀, 5 mat. ♀♀, 11 subad. ♀♀, 12 subad. ♂♂, 3 adult ♂♂, 12 juv.). C. Levings, Swanson Bay (53°N, 128°30′W): 1973 stns. J-1, J-2 (2 mat. ♀♀, 7 subad. ♀♀, 5 subad. ♂♂, 4 juv.); 1975 stns. M-1, M-3, M-5, J-3, JC-1, JC-2, JC-3, JC-5, (1 ov. ♀, 9 mat. ♀♀, 12 subad. ♀♀, 18 subad. ♂♂, 21 juv.). Vancouver Island, Bousfield 1975 stns. P11, P24, P25, P26 (1 ov. ♀, 1 subad. ♀, 2 subad. ♂♂, 5 juv.); Bousfield 1976 stns. B10a, B26, B27, B28 (1 ov. ♀, 1 subad. ♀, 2 subad. ♂♂, 12 juv.); Bousfield 1977 stns. E5, B2, B21b (1 subad. ♂, 5 juv.). British Columbia Provincial Museum Catalogue #68, 48°43.′N, 123°23.8′W, 50 m, silty sand, January 1966 (3 subad. ♀♀, 2 subad. ♂♂, 2 juv.); B.C.P.M. cat. #975-802-99, 49°12′N, 123°58′W, 25 m, 27 June 1921 (1 ov. ♀, 1 mat. ♀, 2 br. II ♀♀, 1 subad. ♀, 1 subad. ♂, 1 juv.).
Southern California, Santa Rosa Island, Allan Hancock Foundation stn. 1390, 80 m (1 mat. ♀).

Diagnosis

(Female): A small *Byblis* (8-10 mm) characterized by: head, anterior margin weakly produced below insertion of antenna 1, eyes present and well developed. Antenna 1, peduncle medium length extending ⅗ length of peduncular segment 4 of antenna 2, flagellum short just reaching end of peduncle of antenna 2. Antenna 2, about ⅔ body length, cone gland of peduncular segment 2 acutely produced. Coxae 1-3, ventral margin strongly serrated. Coxa 1, moderately expanded distally, posterodistal corner not strongly oblique. Coxae 2-3, posterodistal corner not oblique. Coxa 4, posterior tooth moderately produced. Gnathopods 1-2, posterodistal margin of basis serrate. Peraeopod 6, segment 5 bearing well developed comb spines on anterior margin. Peraeopod 7, segment 4 bearing only a single long spine on anterodistal margin, segment 6 with three or four rows of anterior comb spines. Pleonal epimeron 1–2, ventral margin with 4–6 short setae. Uropod 1, rami subequal in size and length, both rami spinulose. Uropod 2, short not reaching tip of uropod 1. Uropod 3, outer ramus slightly longer than inner, medial margin of both rami serrate for middle third and finely serrate on distal third to the tip. Telson, basal width greater than length, tapering distally, apices scalloped with short widely spaced spines, cleft about 1/2 length. Gills in mature females, thin, club-shaped sacs with a few transverse dendritic type pleats.
(Male 8–10 mm): The pelagic male stage differs from the female in: presence of brush setae on peduncle of antenna 1 and 2; gills with longer and more numerous dendritic type pleats; dorsal surface of urosomite 1 with saddle shaped depression proximally and a raised boss posteriorly; uropod 3, rami elongate and evenly serrate for distal 2/3 of medial margin; telson, length 1½ times basal width, apices rounded bearing short subapical spines, cleft about 1/3 length.

Distributional Ecology

Geographic Range: Queen Charlotte Islands to southern California. Bathymetric Distribution: 0–100 m. Sediment Preference: sand.

Life Cycle

Ovigerous females collected during April, May, June, July, and November. Pelagic males collected during June and July.

Remarks

Many records of *Byblis veleronis* from the coastal waters of the northeast Pacific are in fact *Byblis millsi*. In collections from Southern California loaned to the author by the Allan Hancock Foundation, many specimens labelled *B. veleronis* were *B. millsi*. In British Columbia waters, *B. millsi* was found to be much more common than *B. veleronis*. However, both species were found together at some stations. It is surprising that *B. millsi* remained undetected for so long since it differs from *B. veleronis* in its smaller size, length of antenna 1, shape and serration of anterior coxae, structure of gills, length of inner ramus of uropod 1, and serration pattern of uropod 3. *Byblis millsi* does show a high morphological similarity to the bathyal species *B. thyablis*, *B. barbarensis*, and *B. bathyalis* (see Phenogram Fig. 17).

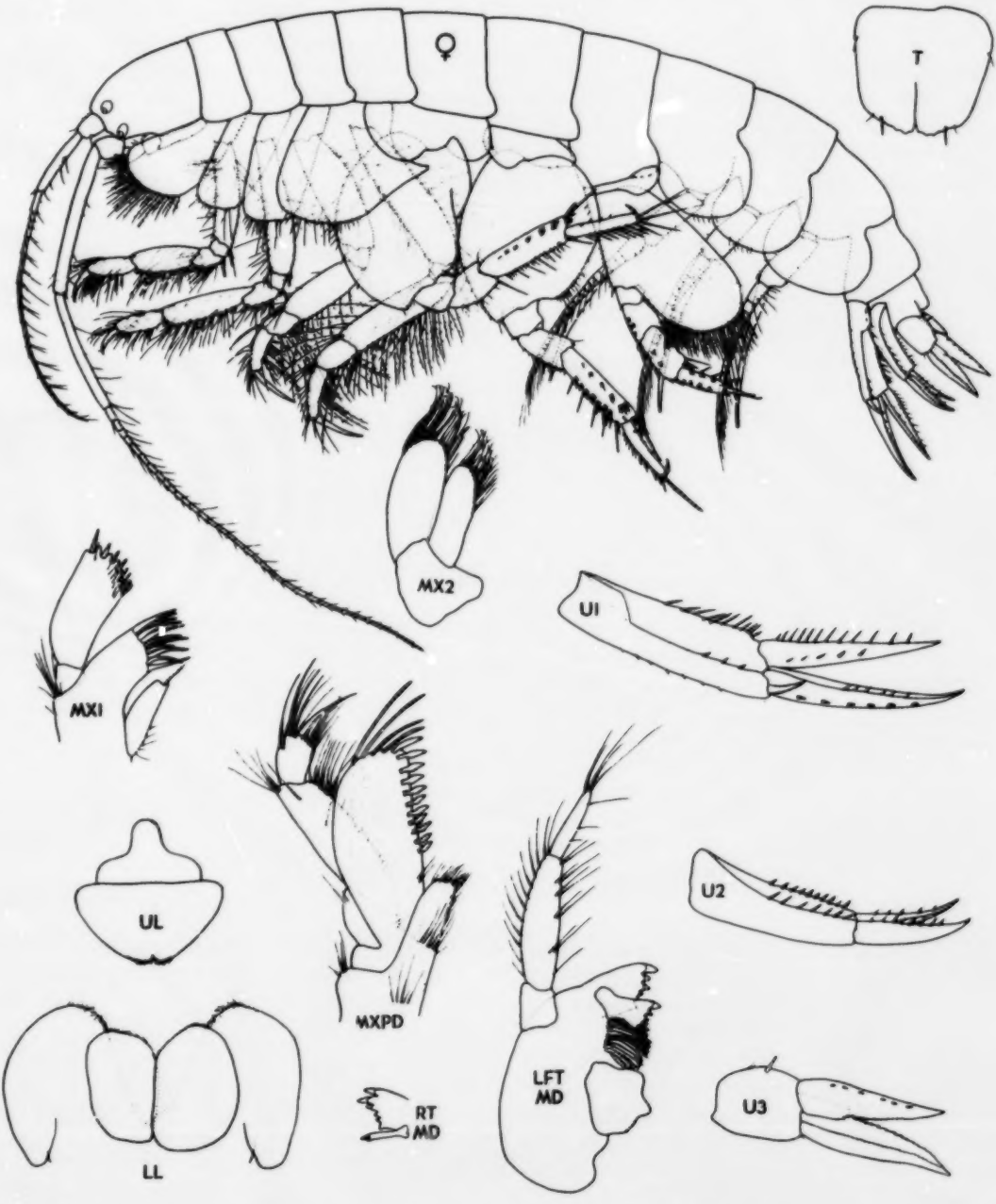

Figure 6. *Byblis millsi* n. sp. Neah Bay, Washington. Bousfield 1966 stn. W39. holotype ♀ 10 mm, ov.

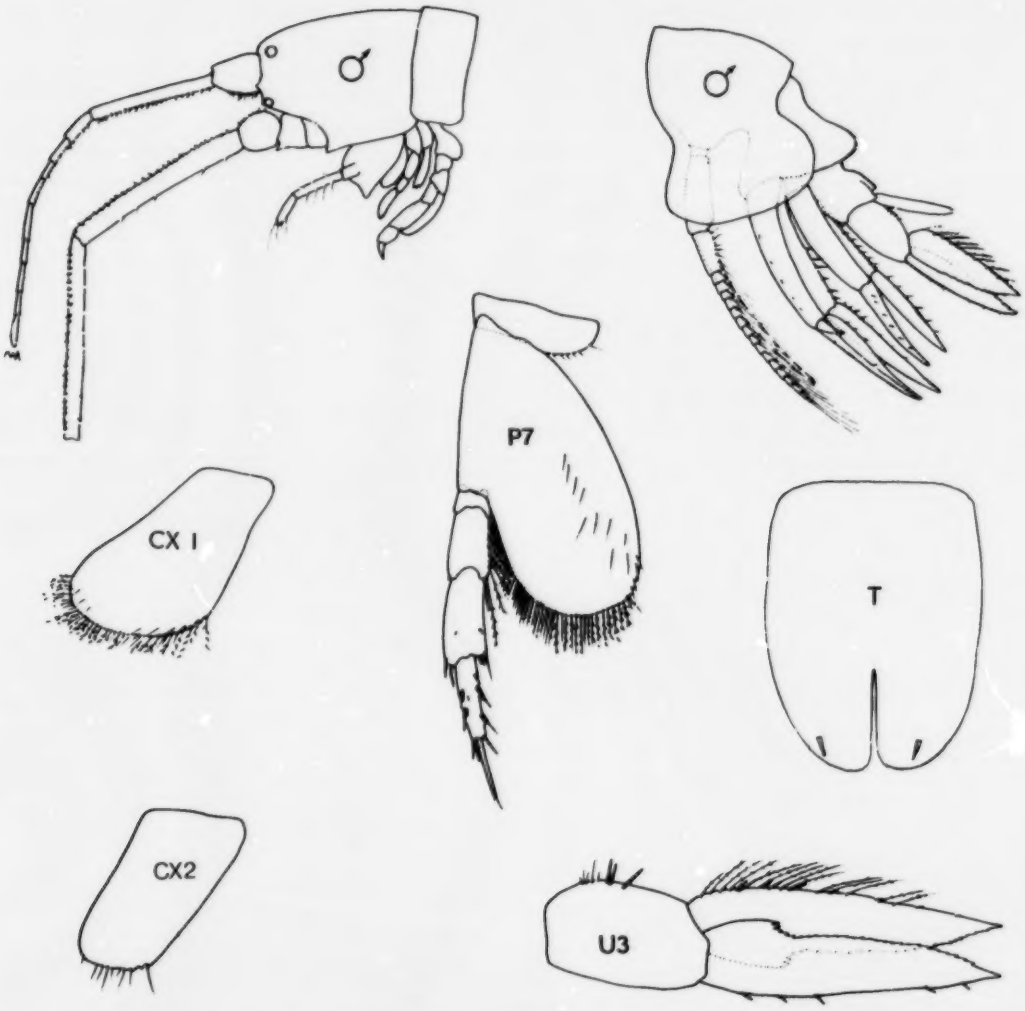

Figure 7. *Byblis millsi* n. sp. Neah Bay, Washington. Bousfield 1966 stn. W39. allotype ♂ 10 mm, pelagic stage adult.

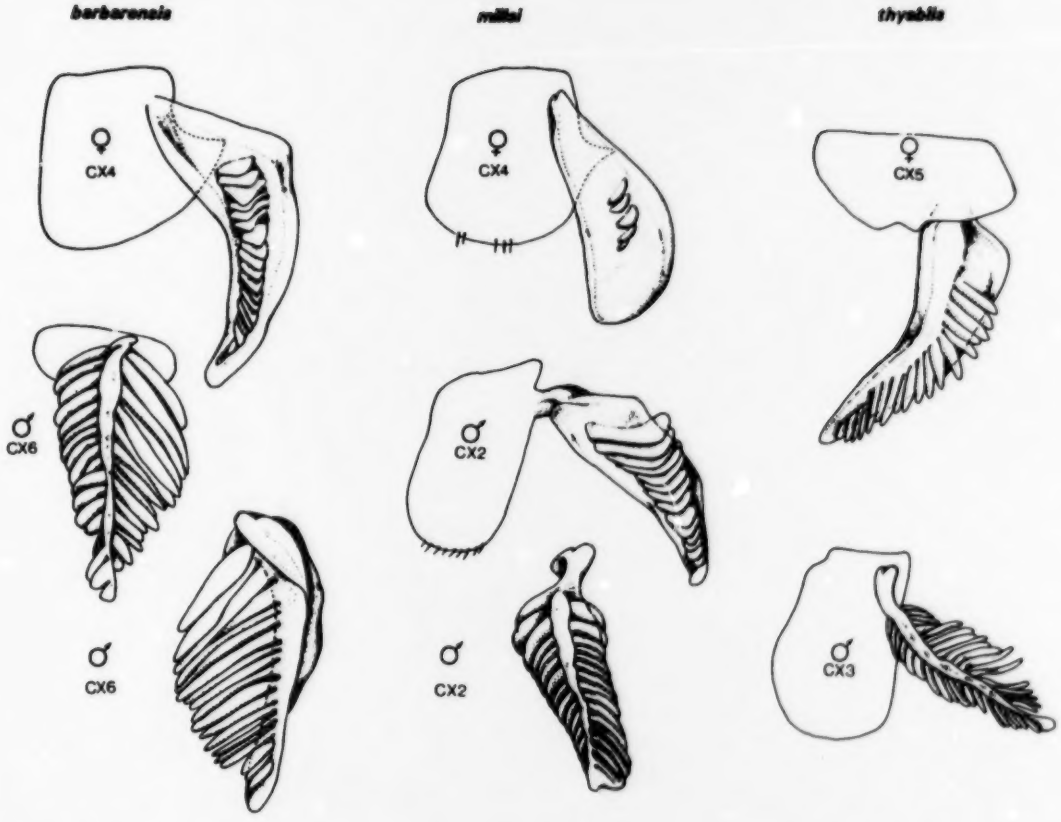

Figure 8. Representative coxal gills of *Byblis barbarensis*, *Byblis millsi*, and *Byblis thyablis*.

Etymology
This species is named after Dr. Eric Mills, Department of Oceanography, Dalhousie University who has made a great contribution to our knowledge of the systematics and ecology of the Ampeliscidae.

Byblis thyablis J.L. Barnard 1971
Figures 8 (in part) & 9

Byblis thyablis Barnard 1971, pp. 4–5, figs. 3-4

Material examined
British Columbia, Queen Charlotte Islands, Kaison Bank, 53°N, 126°W, 198 m, 9 August 1935, British Columbia Provincial Museum Catalogue #976-48-6 (1 mat. ♀, 1 br. II ♀, 2 subad. ♂♂, 1 juv.). **Oregon**, Newport region, 44°40.1'N, 125°6.7'W, 800 m, 18 June 1964, Oregon State Univ. Benthic Invert. Coll. #01340, identified by J.L. Barnard (1 mat. ♀, 3 br. II ♀♀, 1 subad. ♀, 7 subad. ♂♂, 5 juv.).

Diagnosis:
(Female): A small sized *Byblis* (10–11 mm) characterized by: head anterior margin weakly produced below insertion of antenna 1, eyes present and well developed. Antenna 1, peduncle medium length extending 2/3 length of peduncular segment 4 of antenna 2, flagellum very long extending well beyond end of peduncle of antenna 2. Antenna 2, longer than body, cone gland of peduncular segment 2 acutely produced. Coxae 1–3, ventral margin strongly serrate. Coxa 1, moderately expanded distally, posterodistal corner not strongly truncated. Coxae 2–3, posterodistal corner not oblique. Coxa 4, posterior tooth moderately produced. Gnathopods 1–2, posterodistal margin of

basis serrate. Peraeopod 6, segment 5 bearing well developed comb spines on both anterior and posterior margins. Peraeopod 7, segment 4 bearing only a single long spine on anterodistal margin, segment 6 with three or four rows of anterior comb spines. Pleonal epimeron 1–2, ventral margin weakly setose. Uropod 1, outer ramus distinctly longer than inner ramus, both rami spinulose. Uropod 2, short not reaching tip of uropod 1. Uropod 3, medial margin of both rami multi-serrate. Telson, basal width greater than length, tapering distally, cleft about 1/2 length, apices scalloped with short apical spines. Gills, dendritic type.

(Male): Adult pelagic stage males are unknown. Subadult males have longer dendritic type pleats on their coxal gills.

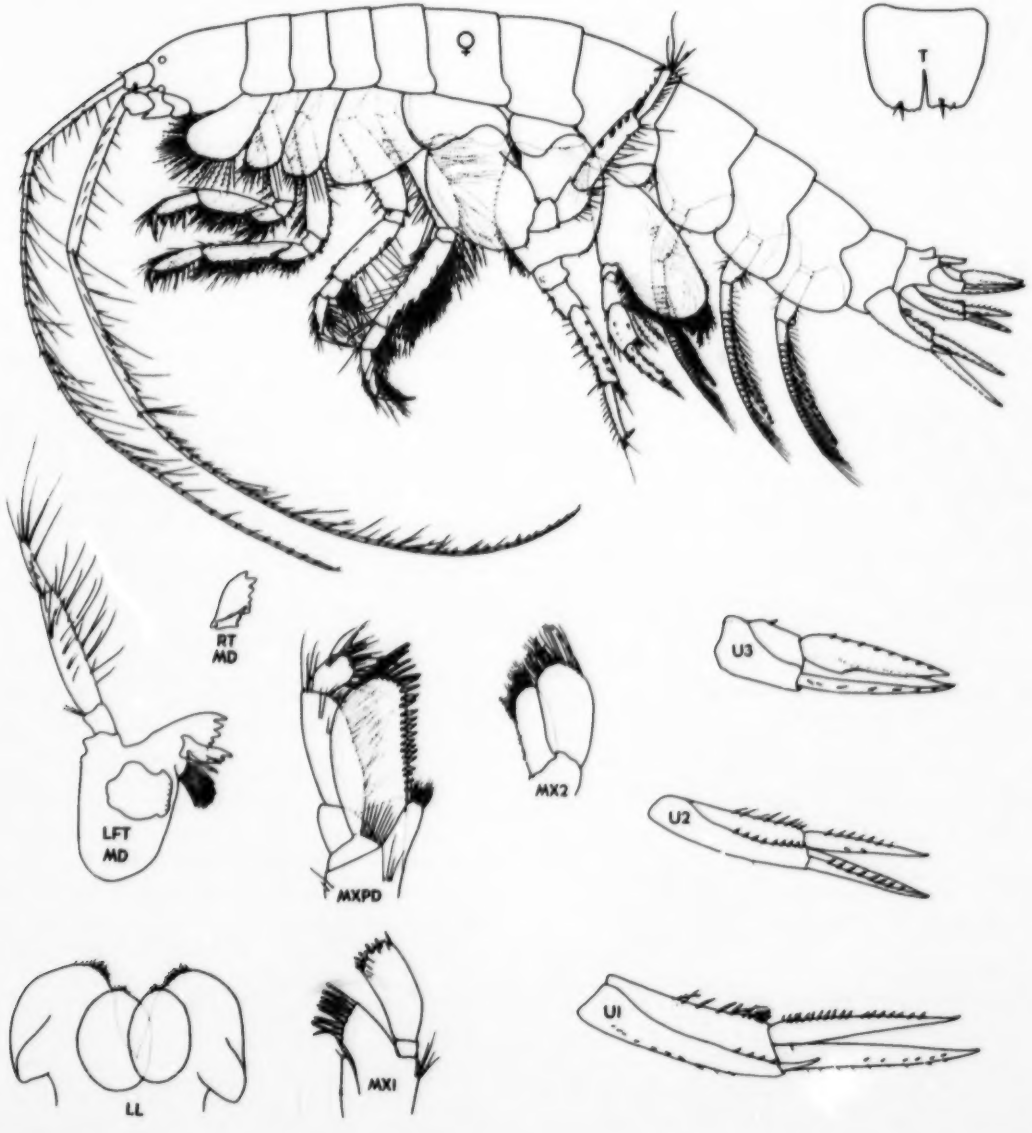

Figure 9. *Byblis thyablis* J.L. Barnard. Kaison Bank, Queen Charlotte Islands, B.C. ♀ 10 mm, mature.

Distributional Ecology
Geographic Range: Queen Charlotte Islands to Oregon. Bathymetric Range: 200–800 m.

Life Cycle
Ovigerous females collected during June and August.

Remarks
B. thyablis is morphologically similar to *B. millsi*, *B. barbarensis*, and *B. bathyalis* (see Phenogram Fig. 17). The separation of *B. thyablis* and *B. bathyalis* seems tenuous, based on Barnard's (1966, 1971) descriptions and figures. Hopefully, a future worker will have the opportunity to re-examine the type specimens, and clarify the status of these species. Barnard's (1971) statement that *B. thyablis* is unique in having sparse setae on the ventral margin of the pleonal epimeron is incorrect. Most species of *Byblis* examined by this author have these setae.

Byblis bathyalis J.L. Barnard 1966

Byblis bathyalis Barnard 1966, p. 58, figs. 3–4
:Barnard 1971, p. 4

Remarks
This bathyal species known from California and Oregon could also occur in British Columbian waters, and is included in the key (see p. 4). It is morphologically similar to *B. millsi* and *B. barbarensis*, and may be identical with *B. thyablis* (see remarks under that species). The condition of its gills is unknown, but it seems likely that they are of the dendritic type.

Byblis barbarensis J.L. Barnard 1960
Figure 8 (in part)

Byblis barbarensis Barnard 1960, pp. 34–35, figs. 11
:Barnard 1971, pp. 3-4

Material examined
Oregon, O.S.U. Benthic Invert. coll. #01465, Coos Bay region, 43°28'N, 124°48.7'W, 534 m, 7 June 1974 (2 mat. ♀♀, 1 br. II ♀, 1 subad. ♂); #01344, Newport region, 44°39.3'N, 124°54.4'W, 800 m, 16 June 1964 (1 mat. ♀).

Remarks
This bathyal species known only from California and Oregon, is likely to occur off British Columbia. *B. barbarensis* shares many morphological characters with *B. millsi*, *B. thyablis*, and *B. bathyalis* (see Table 2 and Fig. 17). Previously unreported is its possession of dendritic type gills (see Fig. 8).

Byblis sp. nr. ***crassicornis***

Byblis crassicornis Barnard 1971, p. 4

Material examined
Oregon, Cascadia Abyssal Plain, 44°41'N, 127°27.5' W, 2820 m, 2 July 1975, O.S.U. Benthic Invert. coll. #01450 (1 mat. ♀); 44°38'N, 125°36'W, 2808 m, 21 June 1973, O.S.U. Benthic Invert. coll. #01449 (1 mat. ♀).

Remarks
Specimens from the same station as Barnard's (1971) material showed enough differences from Sars (1895) illustrations of *B. crassicornis* Metzger 1875 as to suggest that this form should be described as a new species in the future. The shape and armature of the telson were very different. This species is included in the key (p. 4) since it is likely to occur at abyssal depths off British Columbia.

Byblis teres J.L. Barnard 1967

Byblis teres Barnard 1967b, pp. 10–11, fig. 3

Remarks
This species described by Barnard (1967b) from Mexican waters may not occur as far north as British Columbia, but it was included in the key (see p. 4) and the cluster analysis (see Fig. 17) for completeness. It illustrates especially well the mosaic nature of morphological characters in the genus *Byblis*. *B. teres* has characters in common with *B. gaimardi*, *B. veleronis*, and *B.* sp. nr. *crassicornis* (see Table 2), but its overall similarity suggests a relationship with *B. tannerensis* (see Fig. 17).

Byblis tannerensis J.L. Barnard 1966

Byblis tannerensis Barnard 1966, pp. 58–59, figs. 5–6

Remarks
This bathyal species known only from California could occur in British Columbian waters and is included in the key (p. 4). *B. tannerensis* is morphologically similar to *B. veleronis* particularily in the shape of its anterior coxae, but its telson shape suggests that it is not too closely related to that species (Table 2). It would be useful to know the gill type of this species in trying to decide its closest affinities within the genus. Barnard (1966, 1967) suggested that *B. tannerensis* might have its closest relatives in *B. teres* and *B. crassicornis*. This suggestion is supported by the cluster analysis performed on northeastern Pacific *Byblis* (see Fig. 17).

Byblis veleronis J.L. Barnard 1954
Figures 10 & 11 (in part)

Byblis veleronis Barnard 1954, pp. 52–54, figs. 37–38

Material examined
British Columbia, Queen Charlotte Islands, J.W. Scoggan 1965 stn. 104, 54°32′N, 133°25′W, 330 m (1 subad. ♂). North Central Coast, C. Levings: Swanson Bay (53°N, 128°30′W) stns. M-1, M-2, JC-1, JC-4, JC-5, 18 November 1975 (2 mat. ♀♀, 1 br. II ♀, 1 sub. ♀, 6 subad. ♂♂, 3 juv.); Ocean Falls (52°17′N, 127°45′W) stn. 0-4, 75 m, December 1972 (1 subad. ♂).
Mexico, Clarion Island, Sulfur Bay, Allan Hancock Foundation stn. 3914, 9 m, holotype ♀ 14 mm, paratype ♂ 14 mm.

Diagnosis
(Female): A slender bodied, medium sized (14–16 mm) *Byblis* characterized by: head, anterior margin produced weakly below insertion of antenna 1 eyes present and well developed. Antenna 1, peduncle medium length extending about 2/3 length of segment 4 of antenna 2, flagellum medium length extending beyond end of peduncle of antenna 2. Antenna 2, about body length, cone gland on peduncular segment 2 acutely produced. Coxa 1, weakly expanded distally, posterodistal margin strongly truncated obliquely. Coxae 2–3, posterodistal corner strongly oblique. Coxa 4, posterior tooth long, attenuated and acute. Coxae 1–3, ventral margins very weakly serrate. Gnathopods 1–2, posterodistal margin of basis serrate. Peraeopod 6, segment 5 lacking comb spines on anterior margin. Peraeopod 7, segment 4 bearing only a single spine on the anterodistal margin, segment 6 with two rows of comb spines on anterior margin. Pleonal epimeron 1–2, ventral margin with a few short setae. Uropod 1, unarmed outer ramus significantly longer and stouter than spinulose inner ramus. Uropod 2, medium length just about reaching tip of uropod 1. Uropod 3, outer ramus slightly longer than inner ramus, mid portion of both rami coarsely serrate. Telson, basal width greater than length, tapering distally, apices scalloped bearing short widely spaced spines, cleft about 1/2 length. Coxal gills long, thin, club-shaped sacs in mature females (pleated type). (Male–14 mm): The pelagic stage male differs from the female in: presence of brush setae on peduncle of antenna 1 and 2; gills are thicker, shorter, broadly lanceolate, and transversely pleated; urosomite 1, dorsal surface with saddle shaped depression proximally and a raised boss posteriorly; uropod 3, rami elongate with medial margin more finely serrate, inner margin of inner ramus setose; telson, elongate with length 1½ times basal width, apices rounded.

Distributional ecology
Geographic Range: Queen Charlotte Islands to Mexico. Bathymetric Range: 5–300 m.

Remarks
It is difficult to know how common this species is since it has been confused with the newly described *Byblis millsi* by previous workers.

Byblis pearcyi n. sp.
Figures 11 (in part) & 12

Material examined
Alaska, Bering Sea, St. Lawrence Island, 64°50′N, 168°30′W, 7 July 1980, 44 m, collected by U.S. Bureau of Land Management, holotype 17 mm subadult ♂ (NMC-C-1982-15), 2 paratypes ov. ♀♀ (NMC-C-1982-16). Aleutians, 55°18′N, 163°18′W, 46 m, 7 June 1975, U. of Alaska collections (2 juv.).

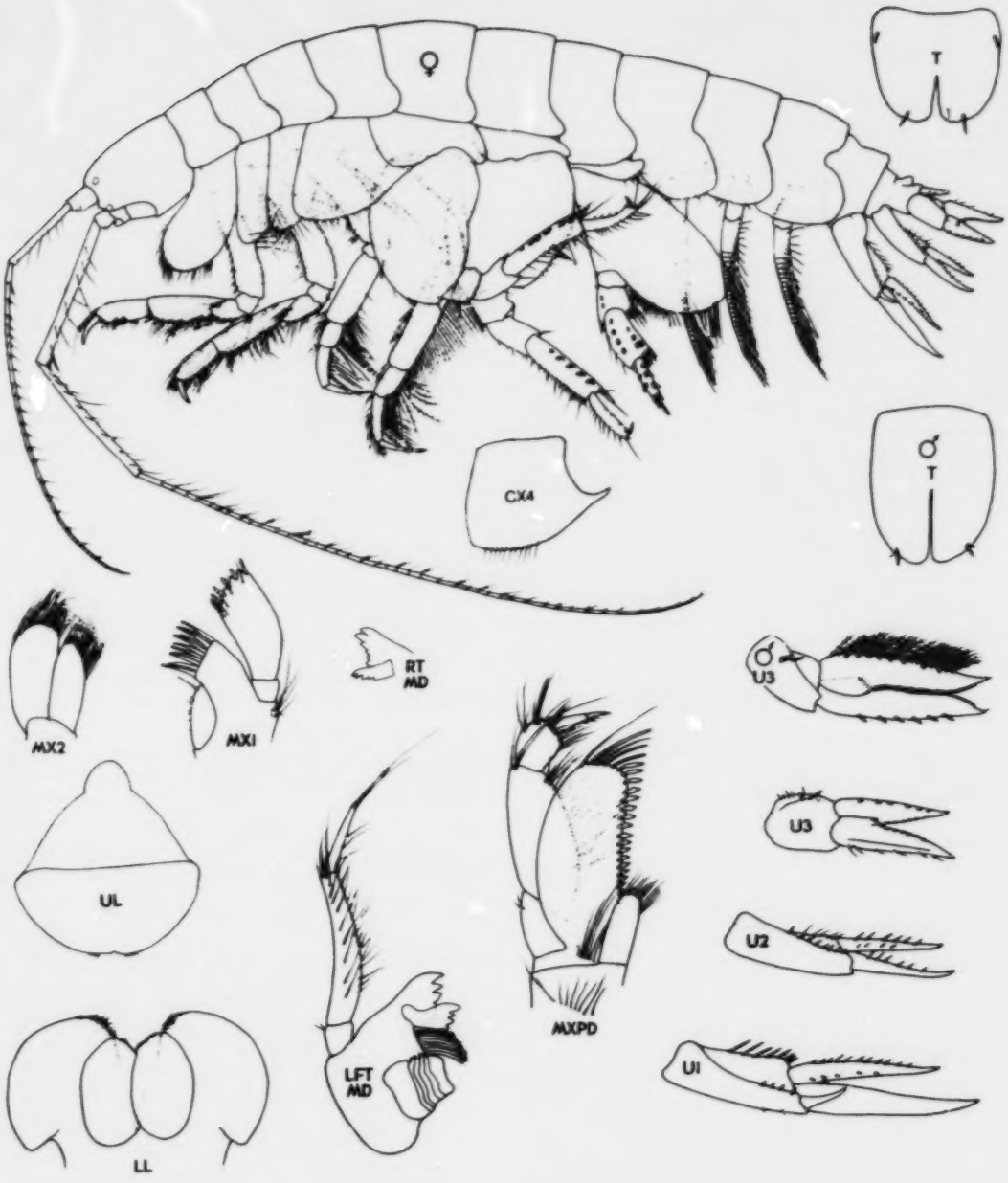

Figure 10. *Byblis veleronis* J.L. Barnard. Swanson Bay, B.C. ♀ 15 mm, br. II. Clarion Island, Mexico. paratype ♂ 14 mm, pelagic stage adult.

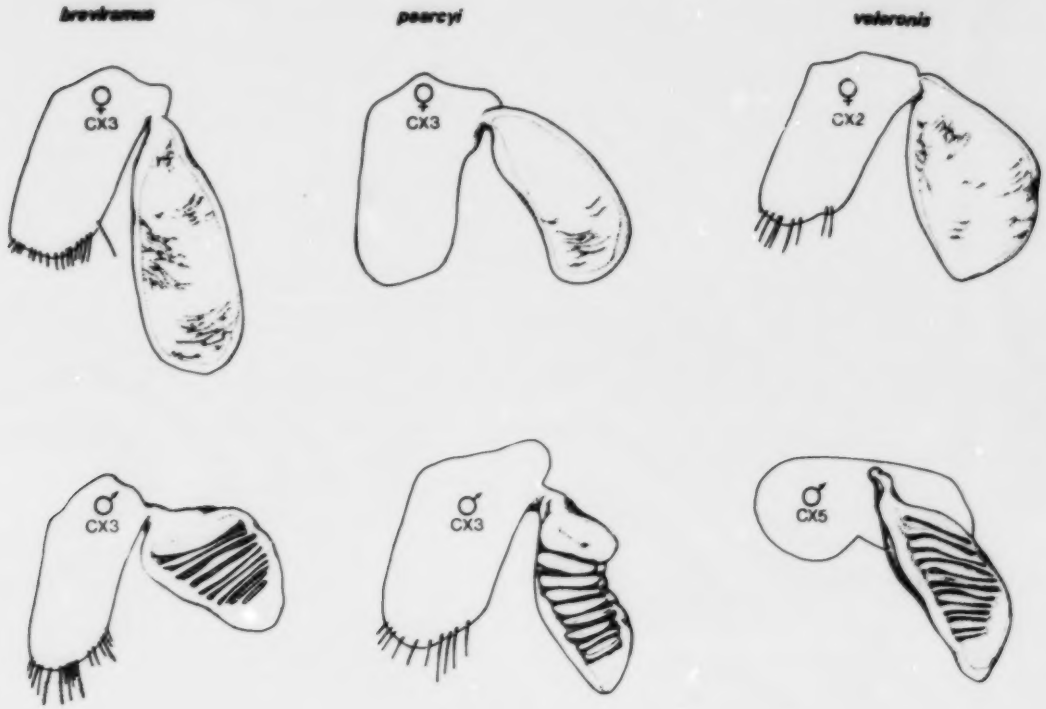

Figure 11. Representative coxal gills of *Byblis breviramus*, *Byblis pearcyi*, and *Byblis veleronis*.

Diagnosis

(Female): A medium-sized (14–18 mm), deep-bodied *Byblis* characterized by: head, lacking process below insertion of antenna 1, eyes present and well developed. Antenna 1, long extending well beyond end of peduncle of antenna 2, peduncle long extending beyond tip of segment 4 of antenna 2. Antenna 2, about body length, cone gland of peduncular segment 2 rounded. Coxa 1, strongly expanded distally, posterodistal margin not obliquely truncated. Coxae 2–3, posterodistal corner not strongly oblique. Coxa 4, posterior tooth moderately produced and acutely rounded. Gnathopods 1–2, posterodistal margin of basis smooth. Peraeopod 6, anterior margin of segment 5 with weakly developed comb spines. Peraeopod 7, anterodistal margin of segment 4 bearing a single long spine, segment 6 lacking anterior comb spines. Pleonal epimeron 1–2, moderately setose on distal margins. Uropod 1, rami subequal and spinose. Uropod 2, medium length just reaching tip of uropod 1. Uropod 3, rami subequal in length, medial margin of rami multiserrated. Telson, basal width equal to length, tapering very little distally, almost square in shape, apices bluntly rounded with short widely spaced spines, cleft about 1/3 length. Gills (pleated type) long, thin, club-shaped sacs in mature females; stouter, shorter, broadly lanceolate and transversely pleated in subadult females and males.

(Male): Adult pelagic stage males are unknown.

Distributional Ecology

Known only from a few scattered localities at mid-shelf depths (40–50 m) in the Bering Sea.

Life Cycle

Ovigerous females collected in July.

Remarks

This species is rather generalized in its morphology, and is not closely related to any other species treated in this study (see Table 2). The cluster analysis suggests that this species may be related to the *B. gaimardi* species group (see Fig. 17), but

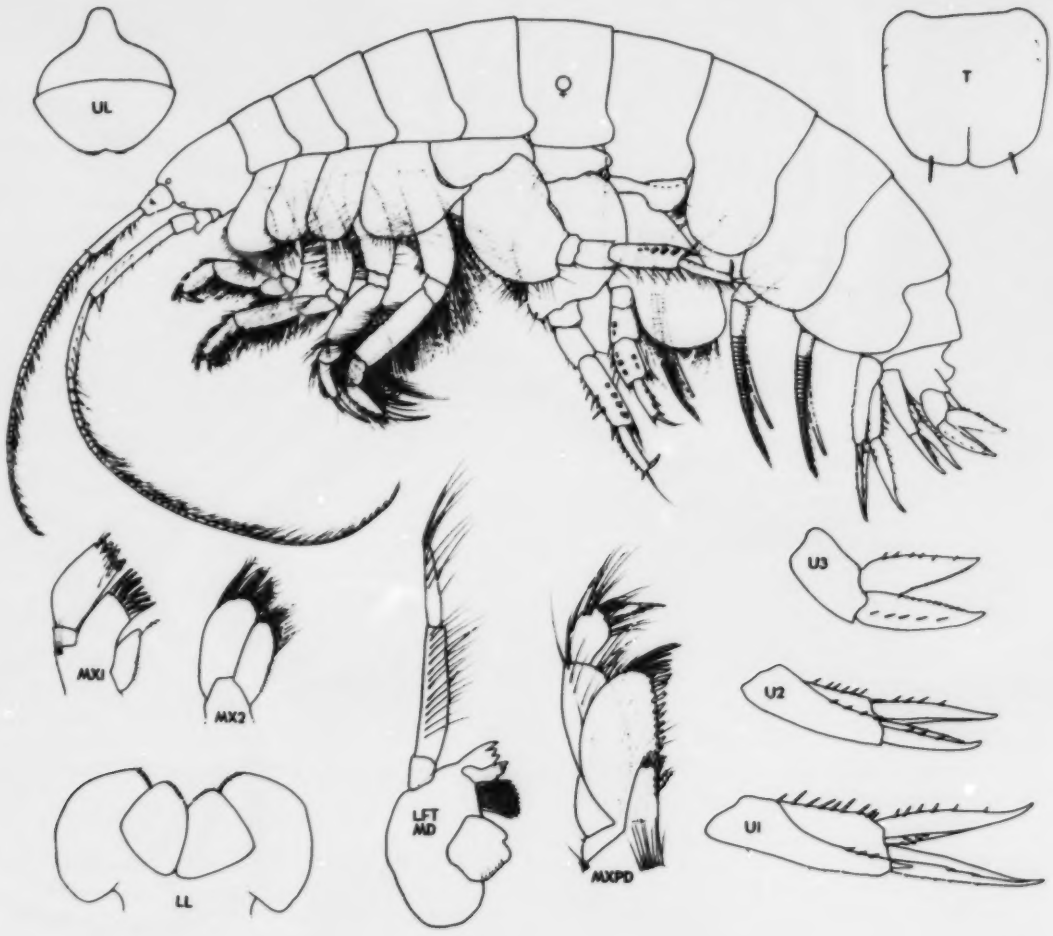

Figure 12. *Byblis pearcyi* n. sp. St. Lawrence Island, Bering Sea, Alaska. holotype ♂ 17 mm, subadult.

its peraeopod 7 and telson are distinctly different from the other species in that group.

Etymology

This species is named in honor of Dr. William Pearcy of the School of Oceanography, Oregon State University, who has contributed greatly to our knowledge of the northeastern Pacific Ecosystem.

Byblis breviramus n. sp.
Figures 11 (in part) & 13

Material examined

Alaska, Bering Sea, St. Lawrence Island, 64°20'N, 168°30'W, 40 m, 7 July 1980, holotype ov. ♀ 28 mm (NMC-C-1982-17), paratypes 2 subad. ♀♀ and 1 subad. ♂ (NMC-C-1982-18).
Additional Material: **Alaska**, Beaufort Sea, O.S.U. Benthic Invert. coll. #01008, 71°13'N, 152°46'W, 40 m, 31 August 1976; #01007, 71°18'N, 152°32'W, 55 m 31 August 1976 (2 br. II ♀♀, 2 subad. ♂♂, 7 juv.). Gulf of Alaska, 59°27.5'N, 145°11.5'W, 3 July 1974, U. of Alaska collections (1 mat. ♀, 4 juv.).
British Columbia, Vancouver Island, Wells Passage, 50°52'N, 126°33.8'W, 150 m, shelly gravel, B.C. Prov. Mus. cat. #980–26 (1 mat. ♀).

Diagnosis

(Female): A large deep-bodied *Byblis* (24–26 mm) characterized by: head, very weakly produced below insertion of antenna 1, eyes present and

well developed. Antenna 1, medium length extending beyond end of peduncle of antenna 2, peduncle stout and medium length extending 2/3 length of segment 4 of antenna 2. Antenna 2, short about 1/2 body length, cone gland on peduncular segment 2 acutely produced. Ventral margins of anterior coxae smooth. Coxa 1, weakly expanded distally, posterodistal margin strongly oblique, distal portion of coxa linguiform in shape. Coxae 2–3, posterodistal corner weakly oblique. Coxa 4, posterior tooth moderately produced and acutely rounded. Gnathopods 1–2, posterodistal margin of basis barely serrated nearly smooth. Peraeopod 6, segment 5 lacking comb spines on anterior margin. Peraeopod 7, segment 4 bearing only a single spine on anterodistal margin, segment 6 lacking anterior comb spines. Pleonal epimeron 1–2, anterodistal margin bearing many long plumose setae. Uropod 1, rami subequal in length and spinulose. Uropod 2 very short, not reaching tip of uropod 1, rami disproportionately short and weakly spinulose. Uropod 3, outer ramus longer and broader than inner ramus, medial margin of both rami serrate for middle third. Telson, basal width greater than length, tapering relatively strongly to tip, apices acutely rounded bearing medium length closely set spines, cleft about 1/3 length. Gills (pleated

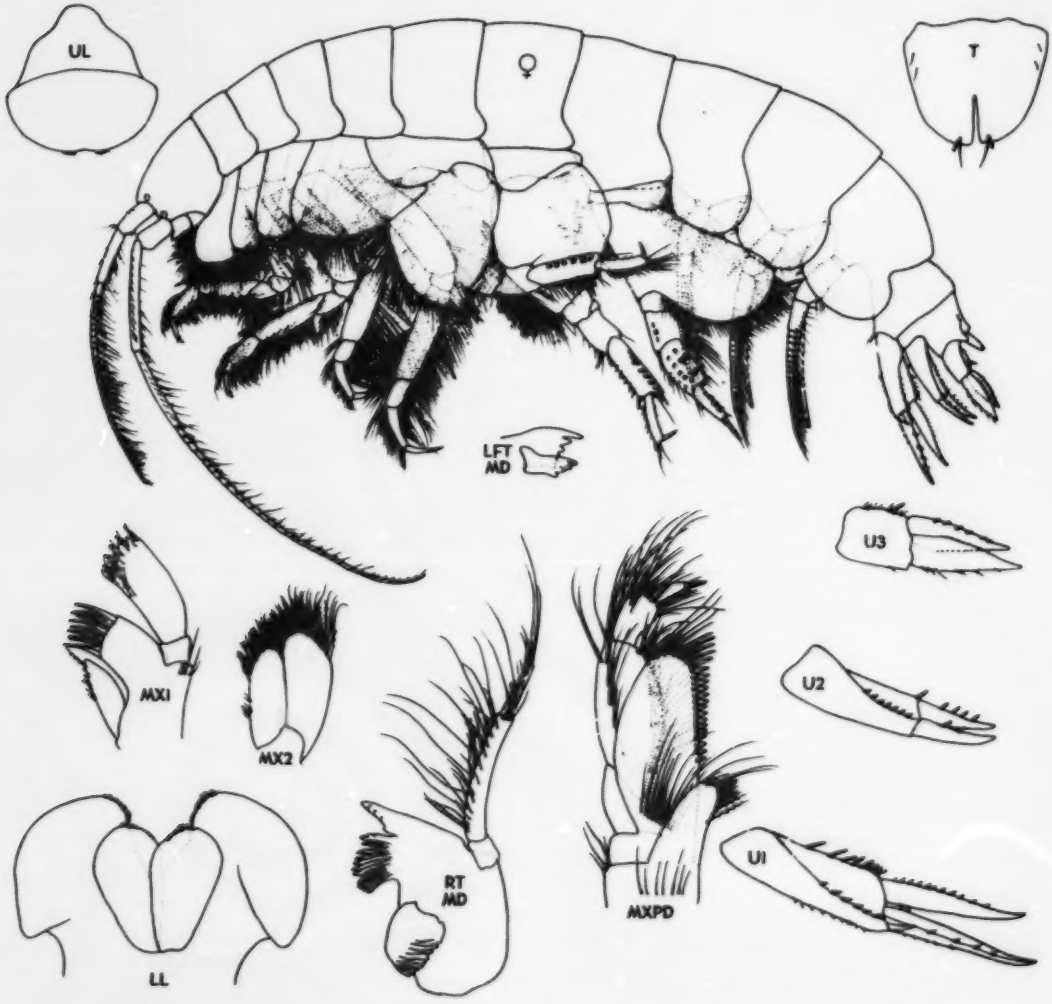

Figure 13. *Byblis breviramus* n. sp. St. Lawrence Island, Bering Sea, Alaska. holotype ♀ 28 mm, ov.

type) long, thin, club-shaped sacs in mature females; thicker, shorter, and broadly lanceolate in subadult females and males.
(Male): Adult pelagic stage males are unknown.

Distributional Ecology
Geographic Range: Beaufort Sea to Vancouver Island. Bathymetric Range: 40–150 m.

Life Cycle
Ovigerous females collected during March, July and August.

Etymology
This species is named for its extremely short rami of uropod 2.

Remarks
The distinct morphology of this species including its very short uropod 2 and fully setose margins of pleonal epimeria 1–2 suggest that it is not closely related to any other northeast Pacific *Byblis* (see Table 2 and Fig. 17).

Genus ***Haploops*** Liljeborg 1856
: Stebbing 1906, p. 116
: J.L. Barnard 1969, p. 132

Diagnosis
Head as deep as long, narrowing only slightly anteriorly. Eyes (when present) usually have lenses only in dorsofrontal pair. Mandibular palp, segments 2–3 usually subequal in length. Maxilliped, inner plate slender and elongate tapering distally. Anterior coxae, medium length. Coxa 1, usually expanded distally. Coxae 2–3, truncated distally. Coxa 4, usually broader than deep with posterior lobe broadly rounded rather than acute. Peraeopods 3–4, segment 5 not greatly reduced in length. Peraeopods 5–6, dactyl medium length and simple. Basal lobe of peraeopod 7, not expanded distally, posterior margin vertical, anterior margin setose near its junction with segment 3. Peraeopod 7, segment 6 usually very reduced in size, dactyl spine-like. Telson, short in female and elongate in pelagic stage male.

Remarks
Barnard (1969) reported 13 described species of *Haploops*. Recent studies by Kaim-Malka (1976) and Wildish and Dickinson (1982) have brought the number of valid species up to 15. Future studies of the deep-sea will add to the world-wide *Haploops* fauna, but this genus probably will never approach the number of species contained in *Ampelisca* and *Byblis*.

Key to the Species of *Haploops* of the Northeastern Pacific Region

1. Basal lobe of peraeopod 7 broad; long setae present on dorsal surface of posterior thoracic segments and pleon ..... *H. setosa* Boeck (p. 27)
   Basal lobe of peraeopod 7 narrow; dorsal surface either smooth or downy but lacking long setae 2
2. Lower front margin of head concave; coxa 1 greatly expanded distally such that maximum width is more than 1/2 length 3
   Lower front margin of head straight; coxa 1 moderately expanded distally such that maximum width is 1/2 or less of length 4
3. Dorsal surface of peraeon and pleon covered with down-like setae; basal lobe of peraeopod 7 expanded distally and obliquely cut; inner ramus of uropod 1 much shorter than outer in females and juvenile males ..... *H. laevis* Hoek (p. 24)
   Dorsal surface of peraeon and pleon smooth; basal lobe of peraeopod 7 lacking distal expansion; coxa 1 posterodistal margin gently rounded; rami of uropod 1 subequal in both sexes ..... *H. sibirica* Gurjanova (p. 27)
4. Antenna 1 subequal to antenna 2 in length; segment 5 of peraeopod 7 produced distally into anterior and posterior lobes; segments 2–3 of mandibular palp subequal in length; dorsofrontal eye with well developed lens ..... *H. tubicola* Liljeborg (p. 23)
   Antenna 1 short just reaching end of peduncle of antenna 2; segment 5 of peraeopod 7 lacking strong distal lobes; segment 3 of mandibular palp much shorter than segment 2; head without ocular lenses ..... *H. lodo* J.L. Barnard (p. 27)

Haploops tubicola Liljeborg 1856
Figures 14 & 15 (in part)

Haploops tubicola Liljeborg 1856, pp. 135–136
: Sars, 1895, pp. 192–194, pl. 67
: Chevreux and Fage, 1925, p. 87, figs. 78–79
: Holmes, 1908, p. 518, fig. 26
: Kanneworf, 1966, pp. 184–191, figs. 1, 2 and parts of 5, 6
: Barnard, 1971, pp. 7–8
Haploops carinata Liljeborg 1856, p. 136 (adult male)
Haploops spinosa Shoemaker 1931, pp. 13–18, figs. 5–6
: Barnard, 1966, pp. 59–60, figs. 7–8

Material examined

British Columbia, Queen Charlotte Islands, J.W. Scoggan 1965 stn. 105, 54°27'N, 131°42'W, 280 m, sandy mud (2 subad. ♂♂). North Central Coast, C. Levings 1972 stn. 0–4, Ocean Falls, 52°17'N, 127°44.8'W, 75 m, 3 December (2 mat. ♀♀, 1 juv.). Bousfield 1965 stn. H37, Open Bight, mouth of Rivers Inlet, 51°23'N, 127°46'W, 65 m, fine sand, July 22 (1 br. II. ♀). Vancouver Island, Howe Sound, 2 November 1976 (1 subad. ♂). B.C. Provincial Museum cat. #8, 18, 20, 38, Satellite Channel, 48°42'N, 123°29.2'W, 76 m, silty sand (1 ov. ♀, 1 mat. ♀, 1 sub. ♂, 3 juv.). **Labrador**, Nain Bay, 56°36.1'N, 61°59.8'W, 30–40 m, silty sand and mud, 21 October 1973, epibenthic sled, collected by E.L. Mills, identified by M.A. Bousfield (1 mat. ♀, 3 br. II ♀♀, 1 subad. ♀, 4 subad. ♂♂, 21 juv.).

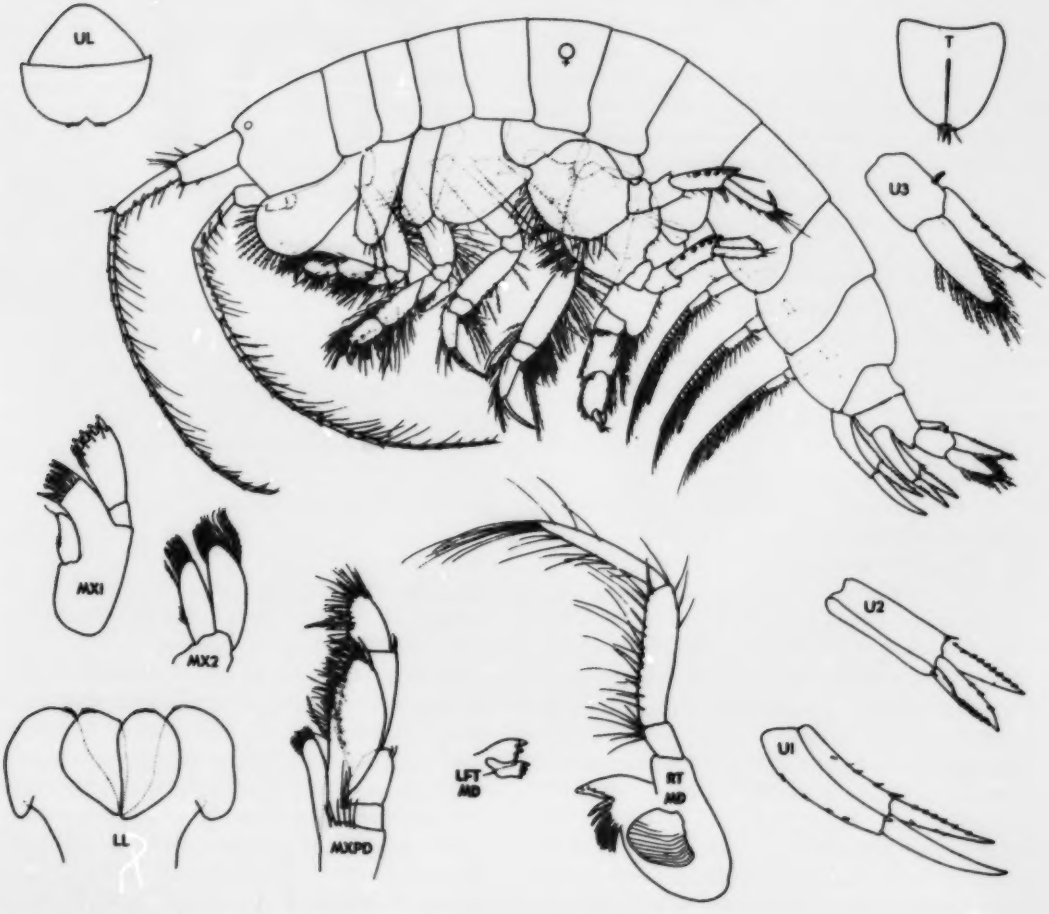

Figure 14. *Haploops tubicola* Liljeborg. Ocean Falls, B.C. ♀ 8 mm, ov.

Diagnosis

(Female): A stout-bodied, medium-sized *Haploops* (8–11 mm) characterized by: head quandrangular, lower front margin straight, only dorsofrontal eyes present. Antenna 1 and 2 subequal in length about 1/2 body length. Mandibular palp, segments 2–3 subequal in length. Maxilla 1, inner lobe bearing a single terminal seta. Coxa 1, moderately expanded distally, maximum width about 1/2 coxa length, ventral margin evenly rounded. Coxa 4, ventral margin nearly transverse, posterior lobe bluntly rounded. Peraeopods 5–6, posterior distal margin of segment 5 produced into a small lobe extending along segment 6. Peraeopod 7, basal lobe narrow with marginal seta along entire posterior edge, distal portion of basal lobe tongue shaped and not expanded, basis over half length of limb, segment 5 produced distally into anterior and posterior lobes. Pleonal epimeron 1–3, distal margin weakly setose, posterodistal corner of sideplates 2–3 produced into a small rounded tooth with a single seta above. Uropod 1, inner ramus spinulose and about 2/3 length of unarmed outer ramus. Uropod 2, rami subequal in length, outer ramus spinulose on both margins, inner ramus spinulose on inner margin only. Uropod 3, inner ramus spinulose on inner margin with apex blunt and setose, outer ramus stouter and setose on both margins. Telson, cleft about 3/4 length. Gills (pleated type) long, thin, club-shaped sacs in mature females; shorter, broader, broadly lanceolate, and transversely pleated in subadult females.

(Male–10 mm): No pelagic males in N.M.N.S. collections. The following diagnosis is based on Sars (1895) and Kanneworf (1966). Pelagic males differ from females in: presence of brush setae on ventral surface of peduncular segments 1–3 and first few flagellar segments of antenna 1 and peduncular segments 3–5 of antenna 2; elongation of flagellum of both antennae with flagellar setae much shorter than in females; coxal gills shorter, thicker, broadly lanceolate and transversely pleated; peraeopod 7, segments 4–5 elongated; uropod 3, rami slightly elongated and more setose; telson elongated such that length equals about 1½ times basal width.

Distributional Ecology

Geographic Range: Circumpolar, south to California in northeast Pacific region. Bathymetric Range: 50–300 m. Sediment Preference: silty sand and silt-clay.

Life Cycle

Kanneworf (1966) found that this species took three years to mature in Danish waters. Mating occurred in August-September, the female carried 40–50 eggs which hatched in January–February. In British Columbian waters, ovigerous females were found in December.

Remarks

Specimens from the northwest Atlantic (Labrador) and the northeastern Pacific were closely compared and no morphological basis could be found to subdivide this species.

Haploops laevis Hoek 1882
Figures 15 (in part) & 16

Haploops laevis Hoek 1882, p. 61, pl. 3, fig. 31
: Stebbing, 1906, p. 117, figs. 28, 29
: Gurjanova, 1951, p. 322, fig. 189
: Barnard, 1961, p. 67
: Kanneworf, 1966, pp. 196–198, fig. 6 in part

Material examined

Alaska, Beaufort Sea, 71°12'N, 152°49'W, 30 m, 11 Nov. 1976, O.S.U. Benthic Invert. coll. #00967 (1 subad. ♂) Bering Sea, St. Lawrence Island, 64°50'N, 168°30'W, 44 m, 7 July 1980, collected by U.S. Bureau of Land Management (1 juv.). **Labrador**, Nain Bay, 56°36'N, 61°59.8'W, 40 m, silty sand and mud, epibenthic sled, 21 October 1973, collected by E.L. Mills, identified by M.A. Bousfield (100 specimens).

Diagnosis

(Female): A large *Haploops* (16–18 mm) characterized by: head, lower front margin oblique and slightly concave, both dorsofrontal and ventrofrontal eyes with lenses although ventrofrontal lenses are small and often difficult to see. Antenna 1 and 2 are subequal and about 1/2 body length. Mandibular palp, segments 2–3 subequal in length. Maxilla 1, inner lobe bearing two terminal setae. Coxa 1, very large, posterodistal margin strongly truncated obliquely. Coxa 4, ventral margin nearly transverse with posterior lobe bluntly rounded. Peraeopods 5–6,

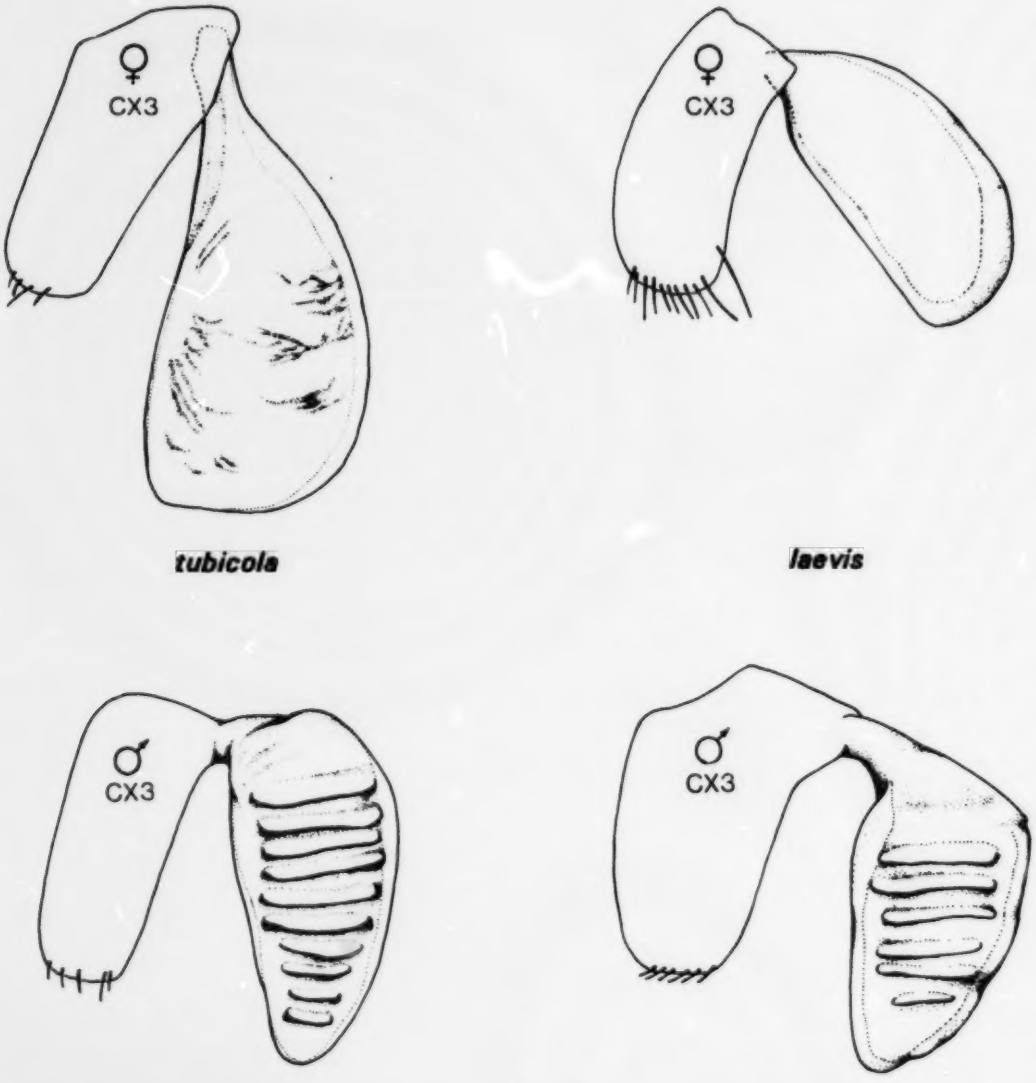

Figure 15. Representative coxal gills of *Haploops tubicola* and *Haploops laevis*.

posterodistal margin of segment 5 produced into a small lobe extending along segment 6. Peraeopod 7, basal lobe narrow with marginal setae confined to truncated portion of posterior margin, distal portion of basal lobe expanded so posterior margin is weakly concave, basis less than 1/2 length of limb, segment 5 produced into anterior and posterior lobes. Pleonal epimeron 1–3, folded into a crease running obliquely posteriorly above ventral margin, distal margins covered with a fine down and bearing moderate numbers of marginal setae. Epimeral plates 2–3, posterodistal corner produced weakly into a small rounded tooth with two setae above it. Uropod 1, inner ramus 2/3 length of outer ramus, both rami unarmed. Uropod 2, rami subequal in length and spinulose on all margins. Uropod 3, inner ramus spinulose on inner margin with apex blunt and setose, outer ramus stouter and setose on both margins. Telson, cleft about 3/4 length. Coxal gills (pleated type) long, thin, club-shaped sacs in mature females; shorter, thicker, broadly lanceolate and trans-

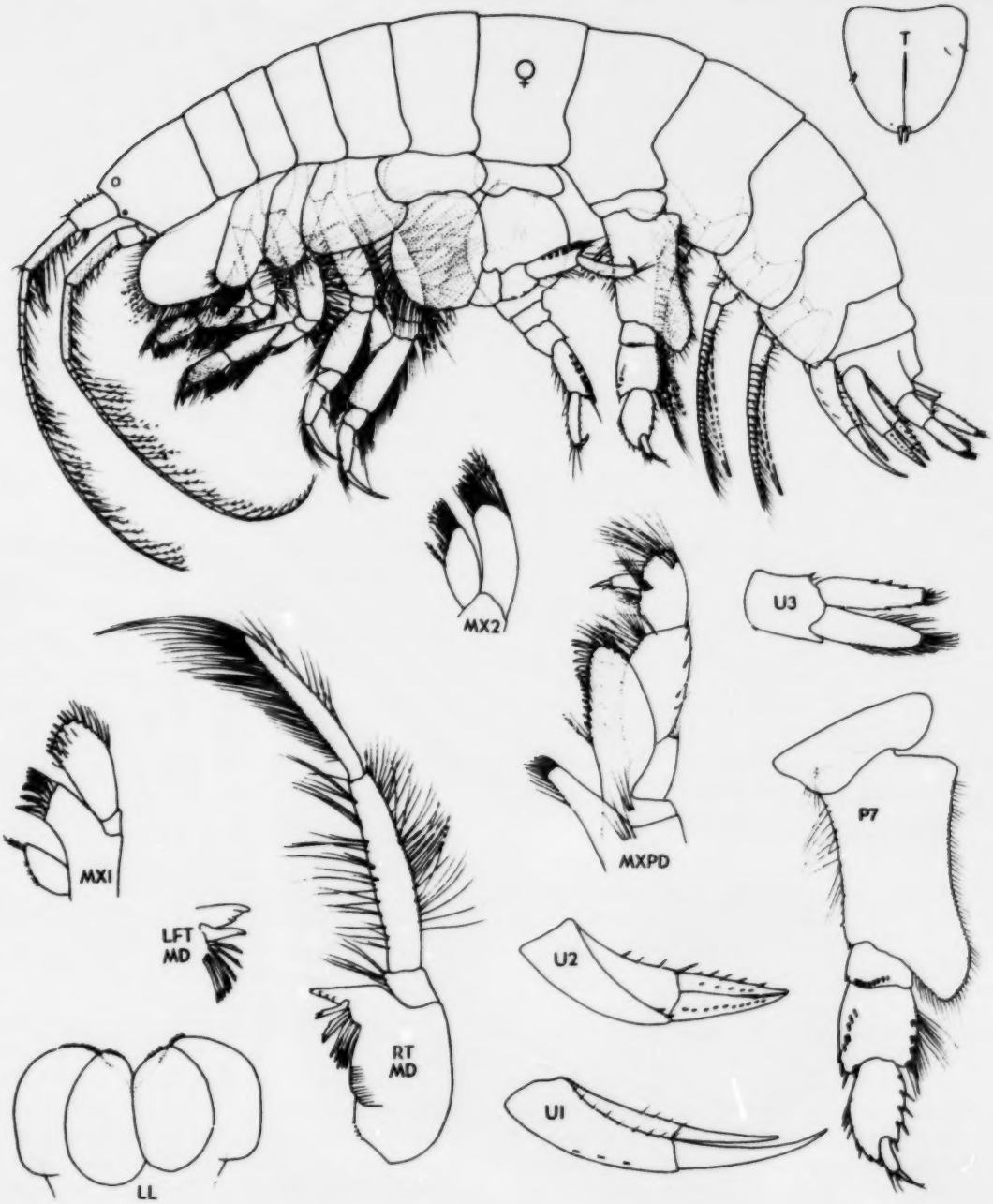

Figure 16. *Haploops laevis* Hoek. Nain Bay, Labrador. ♀ 15 mm, subadult.

versely pleated in subadult females and males. Dorsal surface of peraeon and pleon covered with down-like setae in mature specimens.
(Male): No pelagic stage adult males in N.M.N.S. collections and no existing description in literature.

Distributional Ecology
Geographic Range: poorly known (Kanneworf 1966); in northeastern Pacific, Bering Sea only. Bathymetric Range: 10–500 m (Gurjanova 1951). Sediment Preference: silty sand and mud.

Life Cycle
Unknown.

Remarks
The poor and incomplete descriptions of this species have resulted in much confusion in the literature. Hopefully, the above diagnosis and illustrations will help clarify its status.

Haploops sibirica Gurjanova 1929

Haploops sibirica Gurjanova 1929, p. 315, fig. 7
: Gurjanova, 1951, p. 322, fig. 188
: Kanneworf, 1966, p. 196

Material examined
Alaska, Beaufort Sea, 71°5.2'N, 152°58.7'W, 19 m, 20 August 1976, O.S.U. Benthic Invert. Coll. #00975, A.G. Carey collector (1 ov. ♀, 1 subad. ♂, 3 juv.).

Remarks
Although this species has not yet been recorded from the study area, it is included in the key (p. 22) since it could occur in the region and be easily confused with *H. tubicola* and *H. laevis*.

Haploops lodo J.L. Barnard 1961

Haploops lodo Barnard 1961, pp. 67–69, fig. 38
: Barnard, 1964, p. 18, fig. 13
: Barnard, 1971, pp. 5–7, fig. 5

Material examined
Oregon, Cascadia Abyssal Plain, 44°38'N, 125°36.4'W, 21 June 1973, 2808 m, O.S.U. Benthic Invert. coll. #01415 (1 mat. ♀).

Remarks
This species was included in the key (p. 22) since it is known to occur at abyssal depths (1700–3000 m) in the northeast Pacific region.

Haploops setosa Boeck 1871

Haploops setosa: Sars, 1895, pp. 194–195, pl. 68
: Shoemaker, 1931, pp. 12–13
: Gurjanova, 1951, pp. 323–324, figs. 190–191
: Barnard, 1961, pp. 66–67
: Kanneworf, 1966, pp. 198–200
: Mills, 1971, pp. 378–381, figes. 9b, 11
Haploops robusta G.O. Sars, 1895, pp. 195–196, pl. 68
: Gurjanova, 1951, pp. 324–326, fig. 192
: Barnard, 1961, pp. 66–67

Material examined
Alaska, Beaufort Sea, 70°34.8'N, 144°23.1'W, 71 m, 7 August 1972, O.S.U. Benthic Invert. coll. #00935 (1 br. II ♀, 1 subad. ♀, 5 subad. ♂♂, 1 juv.).

Remarks
Although this species was not found in the study area, it could occur in the Bering Sea and is included in the key (p. 22) for that reason. The best recent description of this species is found in Mills (1971).

Discussion

In an effort to elucidate subgeneric groupings among the species of *Byblis* from the northeast Pacific region, a cluster analysis was performed using the characters listed in Table 1. Each character was defined in such a way that each species could be classified into one of two or three character states depending on the character. This coding process resulted in the data matrix of species vs. characters shown in Table 2. Using this data matrix, a similarity matrix was generated using the simple matching coefficient (see Sneath and Sokal 1973, p. 132). The similarity matrix gives an index of morphological resemblance for each possible species pair. From the similarity matrix, a phenogram (Fig. 17) was generated using the method of complete linkage clustering (see Sneath and Sokal 1973, p. 222). As Dickinson (1982) pointed out, inference of phyletic relationships from such a phenogram should be made cautiously. Although care was taken in defining the characters, both convergence and negative matches can give two species a higher phenetic resemblance than appropriate for their phyletic relationship. However, some useful insights may be gained from a careful examination of the phenogram (Fig. 17).

The phenogram shows four distinct clusters of species: 1) *B. gaimardi*, *B. mulleni*, *B. longispina* and *B. pearcyi*; 2) *B. thyablis*, *B. bathyalis*, *B. millsi*, and *B. barbarensis*; 3) *B. veleronis* and *B. breviramus*; 4) *B.* sp. nr. *crassicornis*, *B. tannerensis*, and *B. teres*. The grouping of *B. gaimardi*, *B. mulleni* and *B. longispina* reflects their high degree of morphological similarity (see Table 2). These three species differ only in the length of antenna 1 and the apical spines of the telson which strongly suggests a close phyletic relationship. The addition of *B. pearcyi* to the *B. gaimardi* cluster is supported by its rounded antennal cone gland and telson shape. However, *B. pearcyi* differs from the other three species in the cluster in several important characters including length of peduncle of antenna 1, number of long spines on segment 4 of peraeopod 7, and length of telson cleft (see Table 2). These differences suggest that the phyletic relationship of *B. pearcyi* to the other three species in the cluster is not close.

The second cluster includes a group of species which have serrated anterior coxae, dendritic gills, spines on anterior margin of segment 6 of peraeopod 7, short uropod 2, and a short, broad telson with scalloped apices (see Table 2). Although not all these character states are exclusive to this cluster, the high overall similarity in the morphology of the *B. thyablis* group suggests a natural phyletic grouping.

The pairing of *B. veleronis* and *B. breviramus* is of doubtful phyletic significance since they differ strongly in such characters as length of uropod 2, and the shape of the telson. Their grouping probably reflects the similarity in the shape of the anterior coxae. The scalloped telson and spination patterns on peraeopod 7 suggest that *B. veleronis* may be distantly related to the *B. thyablis* group. The peculiar combination of characters in *B. breviramus* including its distinctive uropod 2 and fully setose pleonal epimeron suggests that it has no close relations in the *Byblis* fauna of the northeast Pacific region.

The fourth cluster includes species which have a long peduncle on antenna 1, slender distal segments on peraeopod 7, and apically rounded telsons. Barnard (1967) suggested that these three species were closely related, and the cluster analysis performed here supports the validity of his proposal regarding the *B. tannerensis* species group.

Although the cluster analysis has been useful in pointing out possible phyletic relationships among the northeast Pacific species of *Byblis*, it has also underlined the small amount of variability within the genus and the mosaic pattern of characters used to distinguish species (see Table 2). It would have been preferable to analyze the world fauna of this genus, but this proved impossible due to the incomplete descriptions and illustrations available for many of the species. However, since the northeast Pacific species of *Byblis* seem to contain most of the variability represented in the genus, it would seem unlikely that any analysis would result in a formal subdivision of this relatively "tight" genus.

The zoogeography of northeast Pacific species of *Byblis* is summarized in Table 3. Four of the species are arctic forms known primarily from Alaskan waters (*B. gaimardi*, *B. longispina*, *B. pearcyi* and *B. breviramus*). The distribution of species of *Byblis* in the Arctic regions is poorly known, and many new species remain to be

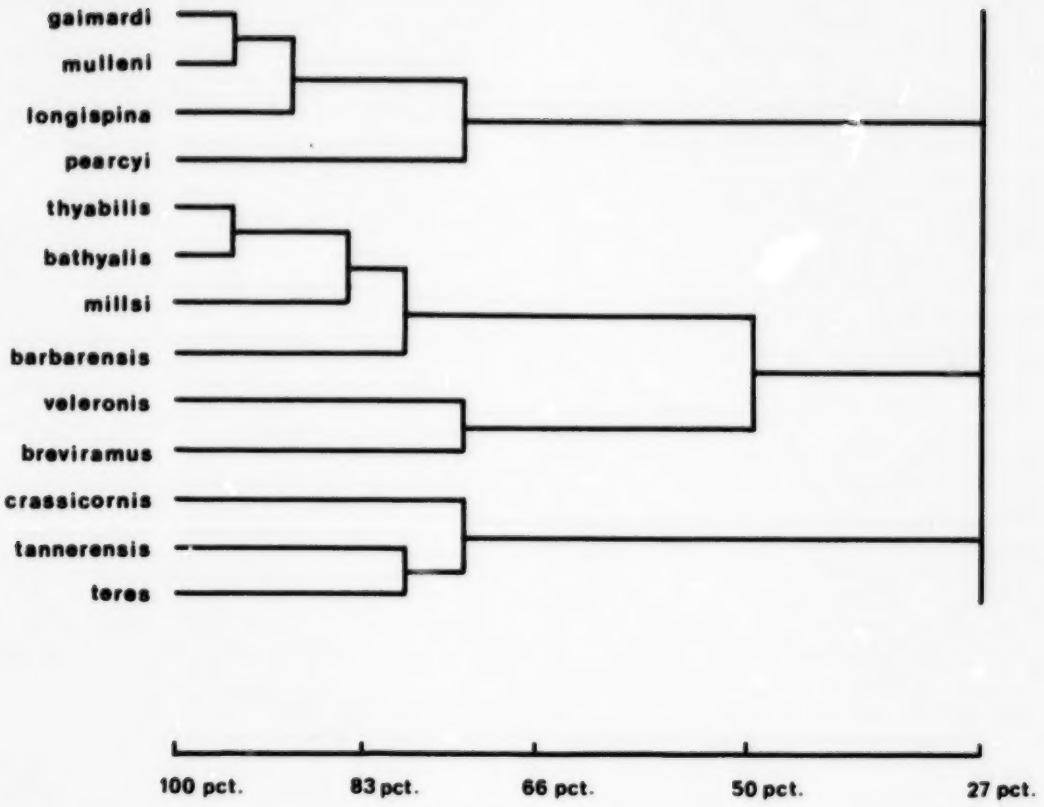

Figure 17. Phenogram showing morphological similarity of species of *Byblis* from Northeast Pacific region. Scale across the bottom is the measure of similarity.

described (J. Just, personal communication). The distribution of bathyal species such as *B. thyablis* is poorly known due to the few collections taken from these depths. *B. veleronis* and *B. millsi* have broad geographic ranges extending from the Queen Charlotte Islands to Mexico corresponding to similar patterns in coastal species of *Ampelisca* from the same region reported by Dickinson (1982).

The richest *Haploops* fauna in the northeast Pacific region occurs in the arctic waters of the Beaufort and Bering Seas where four species have been recorded (see Table 4). The cold temperate waters from southeast Alaska to Oregon are inhabited only by the circumpolar *H. tubicola*. *H. lodo* is known only from abysal depths off Oregon and the Gulf of Panama (Barnard 1971).

It is noteworthy that in *Haploops* only the pleated type of coxal gill has been recorded while in *Byblis* and *Ampelisca* both pleated and dendritic type coxal gills are known (Dickinson 1981, 1982). However, it should be noted that the morphology of the coxal gills is unknown for about half of the described species of *Haploops*.

The limited material of *Haploops* available for this study precluded any attempt to understand phyletic relationships within the genus. This task is better left to a worker with a higher proportion of the world fauna. The material that was available demonstrated that *Haploops* like *Byblis* shows little morphological diversity and a mosaic distribution of character states suggesting that any formal subdivision of this "tight" genus is unlikely to result from future analysis.

The family Ampeliscidae is clearly related to the Dexaminidae (Barnard 1974; Bousfield 1978), but the morphology of this family is quite distinctive particularly in the form of the head and

peraeopods 3–7 which reflect their life style as tube dwelling detritivores. The genera in the Ampeliscidae are easily separable (see key p. 3), but the overall generic diversity in this family is really rather limited when compared to that of other families. This low morphological variability reflects the high degree of uniform specialization required as tube dwellers on sand and mud bottoms.

In an effort to elucidate any strong plesio-apomorphic trends in this family, fourteen characters were selected which varied between the genera of the Ampeliscidae. These characters were defined utilizing two or three character states to include the range of variability found among the genera. Each character state was classified as either plesiomorphic (0), intermediate (.5), or apomorphic (1.0) (see Table 5). This classification of characters was based on out-group comparison and the models developed by Bousfield (1978). Utilizing this multiple character approach, an index of apomorphy could be generated for each of the genera. This index gives a measure of the proportion of advanced and primitive characters in each genus. The possible range of the index for this analysis was 0 (completely plesiomorphic) to 14 (completely apomorphic). The results of this analysis are shown in Table 6.

In contrast to plesio-apomorphic trends within generic groupings of Talitridae and Oedicerotidae shown by Bousfield (1982b, 1982c), the present multiple character analysis revealed no clear plesiomorphic to apomorphic lineage among the genera of Ampeliscidae. *Ampelisca*, *Byblis* and *Haploops* each have an index of 6.0 for the fourteen-character analysis, but each of the three genera are defined by a different mosaic of plesiomorphic and apomorphic characters (see Table 6). The genus *Byblisoides* is slightly more apomorphic with an index of 7.5, based on only twelve characters. Its higher degree of apomorphy presumably reflects its specialized adaptions for life in the abyss. These results suggest that the Ampeliscidae have undergone a relatively recent and rapid evolution which has resulted in a series of mosaic forms rather than a series of living relicts. In order to achieve a greater understanding of both the evolution and ecology of this group, future workers should design studies to increase our knowledge of the functional morphology of these highly specialized tube-dwelling detritivores.

Acknowledgements

This study was made possible by a postdoctoral fellowship from the Natural Sciences and Engineering Research Council of Canada which allowed the author to work in the National Museum of Natural Sciences. I would like to thank the museum staff who provided me with all the necessary facilities to carry out this work. I would especially like to thank Dr. E.L. Bousfield who generously offered continuous advice, stimulating discussion, and critical insight throughout the duration of the study. I would also like to thank Kathleen Conlan, Norma Jarrett, Rama Chengalath, Diana Laubitz, Marjorie Bousfield and Sharon Gowan for helpful discussions. The line illustrations were prepared with the assistance of Floy E. Zittin, Vancouver, B.C.

I would also like to thank Dr. J. Just of the Zoological Museum of the University of Copenhagen for his helpful review of the manuscript.

Table 1. List of Characters Used in Cluster Analysis of Northeast Pacific *Byblis*

1) Length of Antenna 1
   + = short, not exceeding length of peduncle of Antenna 2
   - = long, exceeding length of peduncle of Antenna 2

2) Length of peduncle of Antenna 1
   + = long, peduncle reaching beyond tip of segment 4 of Antenna 2
   - = short, peduncle extending 2/3 length of segment 4 of Antenna 2

3) Shape of cone gland of Antenna 2
   + = rounded
   - = acute

4) Ventral margin of Coxae 1-3
   + = serrate
   - = smooth

5) Shape of Coxa 1
   + = linguiform
   - = distally expanded

6) Posterodistal corner of Coxae 2-3
   + = obliquely truncate
   - = not obliquely truncate

7) Posterior margin of basis of Gnathopods 1-2
   + = serrate
   - = smooth

8) Spination on anterodistal margin of segment 4 of Peraeopod 7
   + = three or more spines
   - = single spine

9) Presence of comb spines on anterior margin of segment 6 of Peraeopod 7
   + = well developed
   - = absent or weakly developed

10) Rami of Uropod 1
   + = unequal
   - = subequal

11) Presence of spines on outer ramus of Uropod 1
   + = unarmed
   - = spinulose

12) Length of Uropod 2
   + = short, not reaching tip of uropod 1
   - = long, reaching tip of uropod 1

13) Medial margin of rami of Uropod 3
   + = multiserrate
   - = single or no serrations

14) Length of Telson
   + = short, length less than basal width
   - = long, length greater than basal width

15) Shape of Telson apices
   + = scalloped
   - = rounded

16) Length of Telson cleft
   + = short, 1/4 telson length or less
   - = long, 1/3 telson length or more

17) Length of Telson apical spines
   + = long, greater than 1/3 Telson length
   - = short, shorter than 1/4 Telson length

18) Presence of Eyes
   + = absent
   - = present

Table 2. Data Matrix of *Byblis* spp. Versus Character States

	Character Number																	
Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
B. gaimardi	–	–	+	–	–	–	+	+	–	–	–	–	+	–	–	+	–	–
B. mulleni	–	–	+	–	–	–	+	+	–	–	–	–	+	–	–	+	+	–
B. longispina	+	–	+	–	–	–	+	+	–	–	–	–	+	–	–	+	+	–
B. veleronis	–	–	–	–	+	+	+	–	+	+	+	–	+	+	+	–	–	–
B. bathyalis	–	+	–	+	–	–	+	–	+	+	–	+	+	–	+	–	–	–
B. barbarensis	+	–	–	+	–	–	+	–	+	+	–	+	+	–	+	–	–	+
B. thyablis	–	+	–	+	–	–	+	–	+	+	–	+	+	+	+	–	–	–
B. millsi	+	–	–	+	–	–	+	–	+	–	–	+	+	+	+	–	–	–
B. pearcyi	–	–	+	–	–	–	+	–	–	–	–	–	+	–	–	–	–	–
B. breviramus	–	–	–	–	+	+	+	–	–	–	–	+	+	+	–	–	–	–
B. sp. nr. *crassicornis*	–	+	–	–	–	+	–	–	–	–	–	–	–	+	–	–	–	+
B. teres	–	+	–	–	+	+	–	–	–	–	+	–	–	+	–	–	–	+
B. tannerensis	–	+	–	–	+	+	–	–	–	+	–	–	+	+	–	–	–	+

Table 3. Geographical Distribution of *Byblis* spp. in the Northeast Pacific Region

Species	Arctic Ocean & Beaufort Sea	Northern Bering Sea	Prince William Sound	Cross Sd. to Dixon Entrance & Queen Charlotte Islands	Northern B.C. & Northern Vancouver Island	Central B.C. & Southern Vancouver Island	Washington & Oregon	California & Mexico
Byblis gaimardi	X	X						
Byblis pearcyi		X						
Byblis longispina			X					
Byblis breviramus	X	X			X			
Byblis mulleni				X			X	
Byblis veleronis				X	X	X	X	X
Byblis thyablis				X			X	
Byblis millsi					X	X	X	X
Byblis barbarensis							X	X
Byblis bathyalis							X	X
Byblis nr. crassicornis							X	
Byblis tannerensis								X
Byblis teres								X

Table 4. Geographical Distribution of *Haploops* spp. in the Northeast Pacific Region

Species	Arctic Ocean & Beaufort Sea	Northern Bering Sea	Prince William Sound	Cross Sd. to Dixon Entrance & Queen Charlotte Islands	Northern B.C. & Northern Vancouver Island	Central B.C. & Southern Vancouver Island	Washington & Oregon	California & Mexico
Haploops setosa	X							
Haploops sibirica	X							
Haploops laevis	X	X						
Haploops tubicola	X	X		X	X	X	X	X
Haploops lodo							X	X

Table 5. List of Characters for Analysis of Genera of Ampeliscidae

1) Relative length of Antenna 1
   0 = subequal to antenna 2
   .5 = reduced
   1.0 = very reduced

2) Length of flagellum of Antenna 2
   0 = flagellum with more than five segments
   1.0 = flagellum with less than five segments

3) Head shape
   0 = quadrangular
   1.0 = elongate

4) Mandibular palp, length of segment 3 relative to segment 2
   0 = segment 2 subequal to segment 3
   .5 = segment 3 distinctly shorter than segment 2
   1.0 = segment 3 very much shorter than segment 2

5) Number of teeth on left lacinia of Mandible
   0 = five cusps
   1.0 = four cusps

6) Presence of eyes
   0 = two pairs subequal
   1.0 = One pair reduced or eyes absent

7) Anterior coxae, length versus width
   0 = moderately deep
   1.0 = very deep

8) Length of segment 5 of Peraeopods 3–4
   0 = normal, longer than deep
   1.0 = greatly reduced, length subequal to depth

9) Dactyls of Peraeopods 5–6
   0 = simple
   1.0 = hooked

10) Degree of Spination on Peraeopods 5, 6, 7
   0 = moderately spinulose
   1.0 = very spinulose

11) Posterior margin of basal lobe of Peraeopod 7
   0 = vertical
   .5 = weakly oblique
   1.0 = strongly oblique

12) Gill Types
   0 = both dendritic and pleated gills present in genus
   1.0 = only pleated gills found in genus

13) Dactyl of Peraeopod 7
   0 = normal, broad at base
   1.0 = reduced to a spine, narrow at base

14) Length of Telson
   0 = long in both sexes
   1.0 = short in females and subadult males

0 = plesiomorphic 0.5 = intermediate 1.0 = apomorphic

Table 6. Multiple Character Analysis of Plesio-apomorphic Trends of Generic Characters in the Family Ampeliscidae.

Character	*Ampelisca*	*Byblis*	*Byblisoides*	*Haploops*
1)	.5	.5	1.0	0
2)	0	0	1.0	0
3)	1.0	1.0	1.0	0
4)	.5	.5	1.0	0
5)	0	0	?	1.0
6)	0	0	1.0	1.0
7)	1.0	0	1.0	0
8)	1.0	0	0	0
9)	1.0	0	0	0
10)	0	1.0	1.0	1.0
11)	1.0	1.0	.5	0
12)	0	0	?	1.0
13)	0	1.0	0	1.0
14)	0	1.0	0	1.0
Index of Apomorphy	6.0	6.0	7.5?	6.0

0 = plesiomorphic. .5 = intermediate.
1.0 = apomorphic. Character numbers refer to Table 5.

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